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FOSSIL PORCUPINE (MAMMALIA, RODENTIA, ERETHIZONTIDAE) FROM EL GOLFO DE SANTA CLARA, SONORA, MEXICO, WITH A REVIEW OF THE TAXONOMY OF THE NORTH AMERICAN ERETHIZONTIDS[1]

DAVID R. SUSSMAN,[2,6] FRED W. CROXEN III,[3] H. GREGORY MCDONALD,[4] AND CHRISTOPHER A. SHAW[5]

ABSTRACT. Among the South American animals that entered North America following the establishment of the Panamanian land bridge were members of the family Erethizontidae. The early fossil record of this group in North America is sparse and so the discovery of fossil porcupines from the Middle Pleistocene (Irvingtonian) fauna of El Golfo de Santa Clara, Sonora, Mexico, provides significant new information on the history of these animals in North America. The taxonomic assignment of the new material required a review of the systematics of North American erethizontids. Based on the most common element preserved, we have restricted our study to features of the dentary that can be used to distinguish the Neotropical porcupine *Coendou* from the North American porcupine *Erethizon*, supplemented by an examination of differences in the caudal vertebrae that also distinguish the two genera. The results of our study lead us to recognize the presence of both *Coendou* and *Erethizon* in the fossil record of North America and to assign the El Golfo fossils to *Coendou* cf. *C. kleini*. We also reassign the taxa *E. poyeri* and *E. kleini*, previously reported from Florida, to the genus *Coendou*. Further, we reassign specimens previously identified as *Erethizon dorsatum* from Irvingtonian faunas in Florida and Aguascalientes, Mexico, to the genus *Coendou*.

In contrast to previous studies in which a linear evolution from *Coendou* to *Erethizon* was proposed, we present an alternative model for the origin of the North American genus *Erethizon*. We propose the existence of two different migration pathways through Mexico. In the west, a branch dispersed north along the north–south mountain ranges into northern North America, resulting in the evolution of modern *Erethizon* in the more temperate part of the continent. In the east, a second branch followed the Gulf Coast into Florida, resulting in the establishment of an eastern population of *Coendou* in the subtropical part of North America, a population that eventually became extinct.

INTRODUCTION

An Early to Middle Pleistocene fauna has been recovered from badlands near the small fishing village of El Golfo de Santa Clara (El Golfo), Sonora, Mexico. The badlands, which cover about 100 square miles, are formed by the erosion of sediments deposited in the delta of the Colorado River at the northern end of the Gulf of California over the past four or five million years (Dorsey, 2006). These sand-dominated sediments, with interbeds of silt, clay, and gravelly sands, were subjected to a series of tectonic uplift events (Colletta and Ortlieb, 1984; Pacheco et al., 2006) followed by water and wind erosion and the consequent exposure of large numbers of vertebrate and botanical fossils (Croxen et al., 2007).

Over the last 20 years, an organized effort to recover these fossils has been undertaken by Professor Fred Croxen and Christopher Shaw under permit from the government of Mexico and under the oversight of the Reserva de la Biosfera Alto Golfo de California y Delta del Río Colorado. At present, about 11,500 individual fossils have been recovered and identified, representing more than 130 different vertebrate taxa. Among these fossils are partial dentaries, teeth, and a single humerus that represent six individual erethizontids, the subject of this paper.

As discussed by Croxen et al. (2007), establishing the exact geologic age of these fossils is difficult. The fossil assemblage is assumed to represent a single paleobiota, but the lack of interbedded ashes prevents determining its age radiometrically. Although studies of the magnetostratigraphy have not produced definitive results, preliminary data suggest that the fossil-bearing sediments are reversely magnetized (F.W. Croxen, personal communication, 2015). If this is the case, the Matuyama reversed epoch (2.588–0.781 Ma) (Cohen et al., 2013) is the only reversal of an age appropriate to the vertebrate assemblage at El Golfo. This assemblage correlates with other faunal assemblages associated with the Irvingtonian North American Land Mammal Age (NALMA) (Bell et al., 2004), particularly with the fauna from the Irvingtonian portion of the stratigraphic sequence at Anza-Borrego State Park in California (Cassiliano, 1999; Jefferson and Lindsay, 2006). Fossils of *Mammuthus meridionalis*, *Megalonyx wheatleyi*, *Nothrotheriops texanus*, and *Sigmodon curtisi* are present, but *Bison* is not and, given the large available sample size, the absence of *Bison* does not seem to be a collection artifact. Some Blancan taxa (*Canis lepophagus, Felis rexroadensis, Sigmodon curtisi*) are present and may be considered remnant populations but suggest an earlier rather than later age for the fauna at El Golfo. However, the presence of *Mammuthus* suggests an age not older than about 1.35 Ma, the earliest well-dated appearance of *Mammuthus* in North America (Bell et al., 2004). With this information, an age range of 0.781 Ma (youngest possible Matuyama) to 1.35 Ma seems a reasonable estimate for the fauna of El Golfo.

Fossil porcupines in North America were reviewed by White (1968, 1970). Based on his examination of a variety of dental

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[1] URL: www.nhm.org/scholarlypublications

[2] Department of Biology, Arizona Western College, Yuma, Arizona 85367, USA.

[3] Department of Geology, Arizona Western College, Yuma, Arizona 85367, USA.

[4] United States Bureau of Land Management, Salt Lake City, Utah, 84101, USA.

[5] Department of Rancho La Brea, La Brea Tar Pits and Museum, Natural History Museum of Los Angeles County, Los Angeles, California 90036, USA.

[6] Corresponding author: David R. Sussman, E-mail: susshotch@gmail.com

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and skeletal features and on measurements in modern and fossil specimens, White concluded that the earliest of these fossil porcupines should be referred to the extant Neotropical genus *Coendou* and that the modern North American genus *Erethizon* evolved in North America from an immigrant species of *Coendou*. The fossil North American erethizontids were subsequently reevaluated by Frazier (1981), including the specimens studied by White plus newly discovered material, and Frazier reached the conclusion that, in contrast to White, all the North American fossils belong in the genus *Erethizon*.

Since the work of Frazier, most researchers have accepted the assignment of fossil North American porcupines to the genus *Erethizon* (e.g., Morgan and White, 1995; Hulbert, 1997; Albright, 1999). Currently, five species of North American porcupines are recognized from the fossil record (Frazier, 1981; Hulbert, 1997). These taxa include *Erethizon bathygnathum* and *E. cascoensis* (which could be considered *bathygnathum*) from western North America, *E. poyeri* and *E. kleini* from Florida, and fossils of the living species, *E. dorsatum*, from several localities in the United States and Mexico. However, there is not complete agreement regarding the generic identification of these fossils and the discovery of the porcupine fossils at El Golfo prompted us to reevaluate the taxonomy of the fossil North American porcupines, in order to assign the El Golfo fossils appropriately.

The ancestors of modern *Erethizon* first entered North America from South America after the formation of the Panamanian land bridge. The timing of the closure of the isthmus, which defines the earliest possible time for the porcupines' entry into North America, is important for understanding their subsequent evolution in North America. Previously, the closure was thought to have occurred around 3.5 Ma. (Webb, 1985; Flynn et al., 2005). However, studies utilizing different dating methodologies, one by Montes et al. (2015) and the other by Bacon et al. (2015), now suggest a more complex and protracted history of closure, possibly beginning in the middle Miocene or earlier, with associated faunal dispersal events in both directions, the last major dispersal event occurring about 6 Ma. These earlier dates, if accurate, create a many-million-year gap (6 Ma or earlier to about 2.5 Ma.) during which porcupines may have entered North America but for which we have no fossil record. Other studies related to the ancestry and early history of North American porcupines include those of Vilela et al. (2009) and Voss et al. (2013), who have proposed, based on mitochondrial molecular clocks, that the lineages ancestral to modern *Coendou* and *Erethizon* separated from a common ancestor at some point during the late Miocene.

Two questions need to be answered regarding Plio-Pleistocene erethizontid fossils in North America. The first, addressed previously by Sussman (2011), relates to the assignment of a 2.5-Ma dentary from the Uquía Formation in Argentina to the genus *Erethizon* by Reguero et al. (2007). The issue is whether the original immigrants to North America had enough morphological traits to assign them to the genus *Erethizon*, as the assignment of the Uquían fossil to *Erethizon* suggests is possible, or whether the distinguishing hallmarks of *Erethizon* evolved after the immigrants entered North America and were exposed to the temperate North American environment. Second, if the morphological traits characteristic of *Erethizon* evolved in North America and are only present in the North American taxon, do any of the North American fossils show traits that might suggest a closer generic relationship to the Neotropical porcupine *Coendou* than to *Erethizon*? The first question is discussed in the previously mentioned Sussman paper (2011), with the conclusion that the Uquían fossil more properly belongs in the genus *Coendou*. The second will be examined here.

The assignment of the porcupines from El Golfo to a genus requires precise definitions of the skeletal and dental characters that distinguish the two living genera and so permit a comparative evaluation of the erethizontid fossils that have been found on both continents.

The extant North American porcupine, *Erethizon dorsatum*, is monotypic. Its distribution includes boreal forests as far north as Canada and Alaska and the forests (and occasionally deserts) of the western, north-central, and northeastern United States, and extends south into the mountainous regions of northern Mexico. Although *E. dorsatum* may be found in open scrub, it prefers forested habitat. It is arboreal and utilizes its muscular tail extensively in its tree-climbing activities. The tail, however, is not prehensile, in contrast to the tail of its Neotropical relative *Coendou*. The diet of *Erethizon* consists preferentially of the leaves and shoots of trees in hardwood forests when available, but it also possesses the well-known ability to eat the cambium layer of tree bark, a trait that allows it to survive winters in deciduous and coniferous forests. Notably, it is the only erethizontid known to have adapted to subarctic conditions and it survives the harsh winters of Canada and the northern parts of the United States not by hibernating but by continuing to forage for food (Roze, 1989).

Subsequent to the arrival of the original immigrants, winters in North America became progressively colder, with the onset ultimately of severe glacial conditions. The substantial metabolic and physical changes evidently necessary to allow a Neotropical porcupine to survive in such an environment form the crux of the argument we propose below that the generic name *Erethizon* must apply only to porcupines that have evolved in North America.

Differences of opinion exist regarding the taxonomy of living South and Central American porcupines. Morphologic and genetic evidence support the conclusion that Neotropical porcupines are monophyletic, with the exception of *Chaetomys* (a morphologically distinct animal with no close living relatives) (Voss and Angermann, 1997; Voss and da Silva, 2001; Voss, 2011; Voss et al., 2013). All Neotropical porcupines (except *Chaetomys*) are included in the genus *Coendou* by Voss. Consequently, *Sphiggurus* and *Echinoprocta* are, in this scheme, considered junior synonyms of *Coendou*. In this paper we follow the nomenclature proposed by Voss.

The extant species of *Coendou* live in tropical and subtropical forests and savannahs of South and Central America. All living species of *Coendou* (13 or more) are substantially smaller in body size than *Erethizon*, with some being quite diminutive. Although knowledge of their natural history is generally sparse, it appears that the ecology of all species of *Coendou* is similar. They eat the flowers, leaves, stems, and fruit of the forests, which are available year round. They may also eat roots, tubers, and insects (Woods, 1984; Emmons and Feer, 1997; Eisenberg and Redford, 1999). Anecdotal reports that *Coendou*, like *Erethizon*, eats bark have not been well documented (L.H. Emmons, personal communication, 2006). They are arboreal and utilize prehensile tails for clinging to branches. As discussed by Voss et al. (2013), even the short tail of *C. rufescens* displays evidence of being prehensile, although it is at the short end of a spectrum of prehensile tail lengths possessed by the various *Coendou* species.

Modern *Erethizon* has been found as far south as southern Sonora and Chihuahua (Jones and Genoways, 1968) and *Coendou* is common in Yucatán and is found as far north as San Luis Potosí on the east side of the Mexican mainland (Emmons and Feer, 1997) and in the state of Michoacán on the west (Monterrubio-Rico et al., 2010), but a distance of several hundred miles in central Mexico separates the modern northern and southern porcupine genera (Fig. 1). This contrasts with the geographically contiguous populations of porcupines that presumably existed after the original dispersal event(s) into North America.

METHODS AND MATERIALS

In order to find consistent anatomical and proportional differences between the two extant genera (*Erethizon* and *Coendou*), we studied numerous examples of modern animals, including nine species of *Coendou* (Appendix 1). We concentrated on dentaries and teeth because these predominate among the El Golfo fossil specimens, are among the most commonly preserved parts of porcupine fossils from other localities, and would seem to have sufficient anatomical complexity to permit the recognition of consistent differences between the genera. Dentaries are also the type specimens for three of the extinct North American species [*E. bathygnathum* (USNM 13684), *E. poyeri* (UF 121740), and *E. kleini* (UF 21473)] and to our knowledge are the only erethizontid fossils from Uquía (MACN 5376) and Tarija (MNHM TAR 695, 696; Hoffstetter, 1963) in South America.

Table 1 provides the dentary measurements we made on modern porcupines, with their averages, ranges, and standard deviations. Where useful, we also performed ratios or multiplied length × width of tooth measurements and these are also shown in Table 1. Values are also shown for the fossils from El Golfo (Table 2), Florida (Table 3), California, Idaho, Aguascalientes (Table 4), and Cumberland Cave, Maryland (Table 5). We examined the caudal vertebrae of porcupines to identify differences between the nonprehensile and prehensile porcupine tails. Although the fossil record is minimal, the differences may be revealing.

Detailed descriptions of how we performed our measurements are found in Appendix 2.

ABBREVIATIONS

ABDSP	Anza-Borrego Desert State Park, California
AMNH	American Museum of Natural History, New York, New York
AWC	Arizona Western College, Yuma, Arizona
DMNS	Denver Museum of Nature and Science, Denver, Colorado
FMNH	The Field Museum of Natural History, Chicago, Illinois
F:AM	Frick Collection, American Museum of Natural History, New York, New York
IGM	Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City, Mexico
IVCM	Imperial Valley College Museum Collection, Anza-Borrego Desert State Park, California
LACM	Natural History Museum of Los Angeles County, Los Angeles, California
LACM (CIT)	Natural History Museum of Los Angeles County, California Institute of Technology, Los Angeles, California
MACN	Museo de Historia Natural de Buenos Aires, Argentina
MNA	Museum of Northern Arizona, Flagstaff, Arizona
MNHN	Muséum National d'Histoire Naturelle, Paris, France
PSM	University of Puget Sound Slater Museum of Natural History, Tacoma, Washington
UF	Florida Museum of Natural History, Gainesville, Florida
UMMP	University of Michigan Museum of Paleontology, Ann Arbor, Michigan
UO	University of Oregon Condon Museum of Geology, Eugene, Oregon
USNM	National Museum of Natural History, Washington, D.C.
ZMUC	Zoological Museum, University of Copenhagen, Denmark

RESULTS

MODERN DENTARIES

In the modern dentaries, we found five traits that are useful in distinguishing the two genera. Refer to Appendix 2 for definitions of terms and measuring techniques. The five traits are listed below.

1. The length of the cheek-tooth row (Fig. 2A): It is immediately apparent that this measurement is definitive in living porcupines. Only the very smallest *Erethizon* equals the very largest *Coendou* in size and there is minimal overlap at those extremes. White (1970:10) found fossil measurements of the cheek-tooth row that fall in the range of modern *Erethizon* but nevertheless assigned these fossils to the genus *Coendou*. Frazier (1981:24–25) included these values (approximately the same as White's) in a classification by discriminant analysis and concluded the fossils should be assigned to the genus *Erethizon*.
2. Ratio of size of p4 to m1: A p4/m1 ratio smaller than about 1.10 indicates *Coendou*, while a p4/m1 ratio larger than about 1.36 indicates *Erethizon*. Although most *Coendou* tend toward smaller ratios and *Erethizon* toward larger, those individuals with a ratio between 1.10 and 1.36 cannot be reliably distinguished by this trait. White (1968:8), measuring only the widths of p4 and m1, arrived at a similar conclusion, while Frazier (1981) did not address this trait.
3. Ratio of anterior–posterior (A-P) diameter to lateral width of lower incisors: In modern adult porcupines, there is an overlap in the ratio of A-P diameter to width between the two genera at 1.2, but incisors with a greater ratio are *Coendou* and those with a lesser ratio are *Erethizon*. Porcupine incisors, in contrast to molars and premolars, continue to grow after eruption in both length and in A-P and lateral diameters for much if not all of the animal's life; this produces a difficulty in using this trait because incisors of *Coendou* appear to lengthen in the A-P direction at a more rapid rate than they widen laterally as the animal grows into adulthood, starting off in newborns with a square (i. e., 1.0 ratio) cross section (PSM 14197, 14201, 14202, 14203) and then progressively elongating in the A-P direction over the next 1–2 years (ratio 1.1: AMNH 262274 with m2 and m3 unerupted, FMNH 14182 with partially erupted m3, LACM 74306 with dp4 and all three molars). The incisors of *Erethizon* retain their juvenile cross-sectional square shape as adults (71 of 75 have ratios of 0.9–1.1). Because of this apparent discrepancy in growth patterns, only animals with permanent p4's (i.e., adults) were included in the analysis.

   While both White (1970:11) and Frazier (1981:14) measured incisors, neither discussed this trait.
4. The orientation of the cheek-tooth row relative to the incisor (Fig. 3): The results of our examination of this trait differ considerably from those of both White (1968, 1970) and Frazier (1981). The reasons for this may relate to the fact that the cheek-tooth row and the incisor on the same side lie in different horizontal and vertical planes and so slightly different measuring techniques or differing rotational positions of the dentary may result in significantly different results. Nevertheless, our technique resulted in 72 of 73 dentaries of *Coendou* having cheek-tooth axes directed lateral to the incisor and one-third of 58 axes directed medially in *Erethizon*. Thus, utilizing our technique, a cheek-tooth axis that runs medial to the incisor in an individual porcupine strongly suggests *Erethizon*, while a large sample of dentaries from a given population of porcupines, all with axes running lateral to the incisor, may suggest *Coendou*. Our results show that modern dentaries of *Erethizon* possess a distinct trend toward anterior convergence of the cheek-tooth rows, a trend not present in the dentaries of modern *Coendou*, in which the cheek-tooth rows remain parallel.
5. The amount of anterior extension (procumbency) of the incisors (Figs. 2B, 2C, 4): As first described by Sussman (2011), the lower incisors of *Coendou* extend anteriorly an average of 7 degrees more than those of *Erethizon*. This difference appears to provide an important means for distinguishing between the two genera. When viewed in conjunction with the tendency for the cheek-tooth rows in *Erethizon* to converge medially toward the incisor and the stronger, square-shaped

cross section of the incisors in *Erethizon*, this trait suggests the possibility of an evolutionary process in *Erethizon*, first noted by White (1970), which provides a strengthened jaw mechanism as compared with *Coendou*.

Other measurements in Table 1, excepting size, do not provide distinctive differences between the genera. In particular, the length of the diastema relative to the length of the cheek-tooth row (the length of the cheek-tooth row should not change once all the teeth have erupted) cannot be used to help diagnose a genus or species because the length of the diastema is variable, being sometimes shorter and sometimes longer than the tooth row. This variation appears to be age (and therefore growth)-related: in *Erethizon*, our measurements show the diastema/tooth-row ratios to be 0.50 in juveniles (n=13), 0.57 in young adults (n=37), and 0.62 in older adults (n=11); in *Coendou* the values are 0.44 (n=8), 0.53 (n=36), and 0.58 (n=52). Thus, on average, older porcupines have longer diastemas relative to the cheek-tooth row compared with those of younger animals.

The angles of scratches on the enamel of the cheek-tooth occlusal surface due to mastication were studied by White (1968), measured from the longitudinal axis of the tooth row. Differences were found between the two genera, providing another diagnostic trait. However, these differences were not considered by Frazier (1981) sufficient to assist in generic identification. Our attempts to examine the scratches suggest that scratches may have multiple angles on the same tooth; curved scratches were also noted, probably because the porcupines do not always chew in a strictly straight back-and-forth or side-to-side motion, but with a circular contribution as well. If this chewing motion is the case, then multiple scratch directions might be expected. In addition, the long axis of individual cheek teeth frequently—but not consistently—varies from the axis of the entire tooth row, producing another difficulty in using these scratches, particularly in isolated teeth. As a result, we conclude that we are not able to utilize the enamel scratches diagnostically.

MODERN TAILS

The number of caudal vertebrae in modern porcupine tails, while variable, appears to depend on whether the tail is prehensile or not. In 19 *Coendou*, we saw tails with as few as 22 and 24 vertebrae, but in most specimens the number ranged from 26 to 34. Thirteen of these tails are from specimens of *C. prehensilis*. We did not see any *Coendou* for which the number of caudals is as small as the numbers observed in the nonprehensile tails of *Erethizon*: 13–17 in 19 tails described by Sutton (1972) and 8–16 by us (n=14). The series of vertebrae in tails of *Coendou* decreases in size gradually in more posterior positions, whereas in *Erethizon* the caudals show a rapid progression from larger to smaller for the length of the tail.

Caudals of *Coendou* have single transverse processes in the most anterior vertebrae, but beginning variably at about the 12th to 15th vertebra, foramina (probably neurovascular) appear in the transverse processes and the processes then gradually progress to complete bifurcation around the 17th to the 20th vertebra. The bifurcations persist for a few vertebrae and then foramina may reappear in the transverse processes of more posterior vertebrae and may or may not persist nearly to the end of the tail (Fig. 5). The exact vertebrae involved in these changes in the transverse processes varies in individual animals, but includes about one-third to one-half of the vertebrae.

We saw no foramina in the transverse processes of caudal vertebrae of modern *Erethizon* and there were no bifurcations in most animals. However, bifurcated transverse processes were observed in one or two posteriorly located caudal vertebrae in a small number of individuals (e.g., MNA Z9.509; Fig. 5D). It is probable that these bifurcated transverse processes in the caudal vertebrae of *Erethizon* are equivalent to, and vestiges of, those seen in the more centrally located vertebrae found in the longer tails of prehensile-tailed ancestors of *Erethizon* prior to the evolutionary loss of the most posterior caudal vertebrae. That is, the trait in Neotropical porcupines that produces the foramina and bifurcated processes may also exist in *Erethizon* but is only rarely observed because of the evolutionary loss of the involved vertebrae.

In the following discussion of the various fossil erethizontid dentaries, we compare the fossils to the five traits we identified as distinguishing modern *Erethizon* from modern *Coendou* as illustrated in Table 6.

SIZE AS A TRAIT TO IDENTIFY A GENUS

Lagoa Santa Fossils versus Shelter Cave Fossils

A large portion of Frazier's argument for assigning all North American porcupine fossils to the genus *Erethizon* is based on a statistical comparison of cranial and mandibular measurements of the fossils with samples of extant *Erethizon* and *Coendou* (Frazier, 1981:21–26). His data demonstrate that the fossils are the same size as *Erethizon*. Similarly, Frazier stated (1981:28) that "(i)ncisor enamel thickness in *Erethizon* is significantly greater than in *Coendou*." Using Frazier's measurements of A-P diameters of incisors and his measurements of enamel thickness, we calculated the percentage of the diameter of the incisors that is enamel and found it to be 5.7% for *Coendou* (0.21mm/3.7mm) and 5.6% (0.27mm/4.8mm) for *Erethizon*. Thus, since the percentage of enamel thickness is virtually identical in both genera, the significantly different absolute values of enamel thickness in the genera reflect only differences in the sizes of the animals, as in the other measurements mentioned here.

In general, we do not accept that size, in and of itself, is sufficient to determine to which of two genera an individual specimen should be assigned. Also needed are significant differences in morphology and function that may reflect significant ecological differences. In contrast, a species of differing size isolated from related species geographically (e.g., *Mammuthus exilis*) or in time (*Coendou kleini* as mentioned below) may be considered a distinct species (but not genus).

To support our contention that the physical differences we found between modern North American and Neotropical porcupines are real and actually distinguish the genera and that they are not related to size, we examined the previously unpublished late Pleistocene/Holocene fossils of *Erethizon dorsatum* from Shelter Cave, New Mexico, and contemporaneous fossils from Lagoa Santa, Brazil (*Coendou magnus*) (Winge, 1888; Hansen, 2012) (Table 7). It is important to note that the fossils from Lagoa Santa are the same size or somewhat larger than modern *Erethizon* and are much larger than any modern species of *Coendou* (Table 1).

Looking at the five distinguishing characters described above, the fossils from Lagoa Santa are about 10% larger than those from Shelter Cave; the single p4/m1 ratio from Shelter Cave is 1.31, high but within the range of modern *Coendou*. The five fossils from Lagoa Santa average a p4/m1 ratio of 1.08 (*Coendou*-only), with three of them falling within the range that is exclusively *Coendou* and two being in the area of overlap of the two genera.

Four out of five adult incisors from Shelter Cave have the cross-sectional shape of *Erethizon* and the fifth is in the area of overlap between the two genera. Three incisors in adult dentaries from Lagoa Santa are either in the area of overlap (n=2) or are

Coendou in shape (n=1). A fourth incisor is in a dentary that retains a dp4 and, as predicted, has a square shape. We examined six isolated incisors and, although we could not definitively determine the animals' ages, the two largest incisors (larger than the others by 2–3 mm in the A-P direction and 0.6–1.7 mm in the lateral direction, thus probably adults) have large ratios (1.4, 1.5) as in *Coendou* and the smaller remaining incisors have ratios of 1.1, with the exception of one that has a 1.3 (*Coendou*) ratio.

The cheek-tooth axes of three fossils from Shelter Cave extend lateral to the incisor; two axes are centered on the incisor. In the dentaries from Lagoa Santa, the axes of all six extend laterally.

All five dentaries from Shelter Cave with measurable incisor angles of procumbency fall into the *Erethizon*-only range. Eight measurements from five individuals from Lagoa Santa all are in the *Coendou*-only range except for one buccal and one lingual measurement, both of which fall within the areas of overlap between *Coendou* and *Erethizon* (Fig. 2D).

An assembled series of disarticulated caudals from the fossils from Lagoa Santa produced a tail with 31 vertebrae. Some of the vertebrae contain foramina in the transverse processes and others show bifurcated transverse processes (Fig. 6). Except for its larger size, the tail appears to us to be identical to that of modern *Coendou*.

In summary, the fossils from Lagoa Santa are larger than those from Shelter Cave. In the remaining traits, measurements that do not fall into the range of overlap between the two genera are, in the case of Lagoa Santa, exclusively in the range of *Coendou* and, for Shelter Cave, exclusively in the range of *Erethizon*. In addition, the porcupines from Lagoa Santa possessed a prehensile tail, a trait found only in modern *Coendou*.

Thus, a comparison of the fossils from Shelter Cave with the fossils from Lagoa Santa shows that our defined characteristics can distinguish the two genera, regardless of size. A large species of *Coendou* lived in South America into late Pleistocene/Holocene times, demonstrating that size alone is not sufficient to diagnose fossil *Erethizon*.

FOSSIL PORCUPINES

El Golfo de Santa Clara

Fossils of porcupine from El Golfo de Santa Clara include the following:

AWC 10858: Right dentary fragment with incisor and m2 and m3; m3 less worn than m2, suggesting a young adult; ascending ramus missing; symphysis and diastema intact (Fig. 7).

AWC 12197: Left dentary fragment with a worn p4; incisor broken off at top of bony alveolus but its diameters are measurable; m1 broken off at top of bony alveolus and occlusal surfaces of m2 and m3 are broken off; most of ascending ramus missing and symphysis and diastema, while mostly intact, have missing portions (Fig. 8).

AWC 13592: Worn right m1 in small fragment of mandibular bone.

AWC 14810: Right dentary fragment with partially broken incisor and m1–3 but missing p4; m3 minimally worn, suggesting young adult; missing diastema, symphysis, and ascending ramus (Fig. 9).

IGM 10199 (collected by H. Garbani *ca*. 1980): isolated broken right incisor.

AWC 12540: Right humerus, about one-third of proximal end missing; epiphyseal suture fully closed, length of fragment 67 mm. Because of the erosion of the compact surface bone, other meaningful measurements cannot be made (Fig. 10).

Measurements of the fossils are provided in Table 2.

Applying the results from our study of modern porcupines to the fossil remains from El Golfo demonstrates the following: The lengths of the cheek-tooth rows of the two measurable El Golfo fossils (AWC 10858 and 12197) are intermediate in size between *E. dorsatum* and *C. prehensilis*, equaling the smallest *Erethizon* and the largest *Coendou*.

None of the fossils had both p4 and an intact m1, so that ratio could not be calculated.

Four fossil incisors could be measured. Two had an A-P/lateral ratio of 1.1 and two were 1.2. Both dentaries with incisor ratios of 1.1 are missing the (d)p4's but have lightly worn m3's (suggesting a young adult), so this measurement provides equivocal results in the fossils.

Two dentaries (AWC 10858 and 12197) have cheek-tooth row axes that run lateral to the incisor, providing inconclusive generic evidence.

AWC 10858 and 14810 have measurable incisor angles of procumbency that fall well within the range of *Coendou*, but are at the highest values for *Erethizon*.

A single p4 and six molars from four different animals all measure either smaller than the smallest modern *Erethizon* or smaller than the mean for *Erethizon*. Two are the size of the largest *Coendou*.

Although incomplete, the humerus is from an adult, appears to be larger than modern species of *Coendou*, and may be about the size of a small *Erethizon*.

No caudal vertebrae from El Golfo have yet been recovered.

In summary, the fossils from El Golfo fall in an intermediate size range between modern *Erethizon* and *Coendou*, have anterior extension of the lower incisors as in modern *Coendou*, and have no traits exclusive to *Erethizon*. They are the same size as *C. kleini* from Florida (discussed below).

Although the porcupines from El Golfo have few distinctive physical traits in the fossils we have found, they do possess the combination of a *Coendou*-type incisor procumbency, laterally directed cheek-tooth axes, and the absence of any traits definitely restricted to *Erethizon*. Additional evidence regarding their identity may be derived from the paleoenvironment of the El Golfo area at the time the porcupines lived. The recovery of remains of fan palm (*Washingtonia* sp.), giant tortoise (*Hesperotestudo* sp.), crocodile (*Crocodylus* sp.), beaded lizard (*Heloderma* sp.), boa constrictor (*Constrictor constrictor*), crested guan (*Penelope* sp.), flamingo (*Phoenicopterus* sp.), and giant anteater (*Myrmecophaga tridactyla*) at El Golfo implies that the annual regional temperature supported tropical to subtropical environments (Mead and Shaw, 2011; Shaw et al., 2013).

Steadman (2011) notes that, regarding the avifauna of El Golfo, "[t]he more tropical biogeographic affinity of some of the birds agrees with that suggested for certain associated reptile and mammal fossils." This subtropical ecosystem, of which the El Golfo porcupines were a part, supports our interpretation that they are *Coendou* and not *Erethizon*, based on the known habitat differences of the two modern genera. There do not appear to be any convincing reasons to think that the fossil porcupines at El Golfo were preadapted for cold-weather tolerance or that they subsequently acquired it while living in a subtropical climate, cold-weather tolerance being a defining characteristic of living *Erethizon*.

The temporal and physical isolation of the porcupines at El Golfo from the other fossil porcupines in North America raises the possibility that they were part of a dispersal event to North America distinct from that of earlier dispersals. As a group, their size—somewhat smaller than other early to mid-Pleistocene fossil porcupines, except for *C. kleini* in Florida, and smaller than modern *Erethizon* but larger than extant *Coendou*—perhaps represents an intermediate stage in a diminution in size of *Coendou* that apparently occurred at some point during the Pleistocene but for which we know of no South American fossil record.

We conclude that the El Golfo porcupines should be assigned to the Neotropical genus *Coendou* and further, due to their overall similarity to *C. kleini*, we assign them to *Coendou* cf. *C. kleini*, pending the discovery of more diagnostic material to help clarify the species designation.

Florida

We examined porcupines from late Blancan and Irvingtonian faunas from five sites in Florida previously identified as *Erethizon poyeri* (found at Haile 7C, *ca.* 2 Ma) (Hulbert, 1997), *E. kleini* (Inglis 1A, ca. 1.9 Ma) (Frazier, 1981), *E. dorsatum* (Haile 16A, ca. 1.6 Ma.) (Morgan and White, 1995), *E. dorsatum* (Leisey 3A, ca. 1.5 Ma.) (Morgan and White, 1995), and *E. dorsatum* (Coleman 2A, 0.6–0.3 Ma.) (Morgan and White, 1995). See Table 3 for measurements.

The lengths of the cheek-tooth rows are long, at or above those of *Erethizon*, except for two fossils from Inglis 1A, which are somewhat smaller, falling between the sizes of modern *Coendou* and *Erethizon*.

The *E. poyeri* fossil (UF 121740) has a p4/m1 ratio of 0.96, in the range of modern *Coendou*. The four other measurable fossils all have larger ratios, none of which exceed the range of *Coendou*, but trending toward *Erethizon*.

Three incisors have A-P/lateral ratios of 1.1 and one has a ratio of 1.2. Of the three with ratios of 1.1, one has worn molars (UF 21473), suggesting an older adult, one has a broken (d)p4 and lightly worn m1 and m2 but is missing m3, possibly a juvenile or young adult (UF 135669), and the third has an unworn p4 and lightly worn m1 and m2, a young adult (UF 21490). With the exception of the single older adult, these measurements are not diagnostic.

The axes of six cheek-tooth rows relative to the incisor, representing three of the five sites we studied, are measurable (Fig. 11). All six axes run lateral to the incisor, a feature that is characteristic of *Coendou*. Our findings contrast with those of Morgan and White (1995) that the axes of the Leisey 3A cheek-tooth rows run medial to the incisor. We found that, using our method of analysis (see Appendix 2), UF 124632 has an axis that is directed laterally (Fig. 11); in UF 135669, the incisor alveolus and the alveolus of p4 are both broken, making a measurement unreliable.

Six measurements of incisor angle of procumbency (from four fossils, representing three sites) all fall in the range of *Coendou*, are greater than the range of *Erethizon*, and all but one are greater than the mean for *Coendou* (Figs. 2F, 2G, 12).

The sizes of the p4's and molars in the Florida fossils, as judged by the product of length times width, all fall within or slightly above the range for modern *Erethizon*, with the notable exception of *E. kleini*. Three dentaries of *E. kleini* and their individual teeth have measurements close or equal to those of the fossils from El Golfo (see above) and are intermediate between modern *Coendou* and *Erethizon*. This intermediate size was the primary distinguishing feature used by Frazier (1981) to designate them as a new species (Fig. 2E).

A previously undescribed specimen of *E. poyeri* from Haile 7G was preliminarily reported by Hastings et al. (2006). It includes eleven caudal vertebrae, some of which were noted to have bifurcated transverse processes ("dual transverse process sets") and from those vertebrae the investigators estimated the original length of the tail at "26–32 caudal vertebrae." In addition, eight other skeletal traits "are preserved well enough in this new specimen for study and all plot within the range of *Erethizon*." While not explicitly stated, these traits presumably relate to the size of the animal. We have not been given access to this fossil and so cannot at this point make an independent judgment regarding its taxonomic assignment.

Except for size and the one incisor ratio, none of the studied traits in the fossils from Florida fall into a range exclusive to *Erethizon*. The large p4/m1 ratios trend towards *Erethizon* but there are modern *Coendou* with the same ratios. On the other hand, the small p4/m1 ratio of *E. poyeri* falls well within the range of *Coendou*. The six tooth-row axes, all directed laterally, suggest *Coendou*, because in a population of *Erethizon* one or two axes could be expected to be medial.

The strongest evidence in the Florida fossils is found, first, in the incisor angles of procumbency, which are uniformly in the range of *Coendou*, and, second, as described by Hastings et al. (2006), in the presence in the caudal vertebrae of bifurcated transverse processes accompanied by the suggestion of approximately 30 total vertebrae—in other words, a prehensile tail, a distinguishing trait of modern *Coendou*.

The porcupines from Florida we examined show no evidence of the mandibular modifications present in modern *Erethizon*, that is, the anterior convergence of the cheek-tooth row relative to the incisor and the more acute angle of incisor procumbency in *Erethizon*. These modifications we interpret as helping to allow *Erethizon* to survive in northern climates by eating the cambium of trees when no other food is available. Except for their larger size, the fossil porcupines from Florida cannot be distinguished from modern Neotropical *Coendou*. We therefore conclude there is sufficient reason to reassign the Florida porcupines found at Haile 7C, Haile 7G, Inglis 1A, Leisey 3A, and Haile 16A to the genus *Coendou*. We assign the nondiagnostic Coleman 2A dentary fragment to *Coendou* also, as a relict population, acknowledging that its young age may represent instead a southern range extension of *Erethizon*.

The fossils from Inglis 1A were described as a new species (*E. kleini*) by Frazier (1981) based on their size, which is somewhat smaller than the other fossil porcupines from Florida. The fossils from El Golfo described above are the same size as *C. kleini*. However, because several hundred thousand years and two thousand miles separate the two populations, the strength of the relationship between the two groups can be questioned. Still, the existence of two separate populations of smaller fossil porcupines at least suggests that *C. kleini* from Florida and *Coendou* cf. *C. kleini* from El Golfo may represent distinct South American dispersals into the North America.

Western North America

Aside from the fossils from El Golfo, we examined fossils from faunas in the western United States: Grand View from Jackass Butte, Idaho (*ca.* 2.0–2.3 Ma) (Wilson, 1935; Shotwell, 1970; Repenning et al., 1995; Bell et al., 2004), and Vallecito Creek and El Casco, California (Table 4). Work by L. K. Murray (personal communication, 2011) restricted all of the Vallecito Creek erethizontid fossils to the C2r.1n geomagnetic chron (1.9–2.2 Ma). The fossils from El Casco have a similar age, with the exception of a single broken tooth from an adjacent site (the San Timoteo Badlands) that may, along with a tooth from Wolf Ranch in Arizona (Harrison, 1978; Lindsay et al., 1990), be among the oldest of the erethizontids in North America at 2.5 ± Ma (Albright, 1999; Bell et al., 2004).

Our measurements indicate that the lengths of four cheek-tooth rows (two from Idaho and two from California) equal or are slightly larger than the lengths of modern *Erethizon*. Only two p4/m1 ratios could be determined, both on the fossils from Idaho. One (USNM

13684) is quite large but not beyond the range of modern *Coendou*; the other falls into the range of overlap between the two genera.

Three incisors from Idaho have cross-sectional ratios of 1.0 and 1.1; one of these is an adult (USNM 13684), one a juvenile (UO F-16272), and the third (UO F-16271) is a young adult. Three fossils from El Casco and Vallecito Creek have ratios of 1.0, a fourth is 1.1, but the ontogenetic ages of the animals cannot be determined. Although none of these incisors have a ratio in the range of *Coendou*, the inability to determine the ontogenetic age in the majority of them prevents a definitive assignment to *Erethizon*.

Three cheek-tooth axes are all directed laterally, which is uninformative.

UO F-16271 from Jackass Butte, Idaho, has a lingual angle of incisor procumbency of 132 degrees, a trait of *Erethizon* that is well outside the range of modern *Coendou* (Fig. 12). Unfortunately, it is the only fossil in which the angle is measurable.

A fossil from Vallecito Creek, ABDSP (LACM) 1563/V6136 (LACM 6136 in Frazier, 1981) has a number of caudal vertebrae associated with it. Jefferson and Murray (G.T. Jefferson, personal communication, 2010) determined that there are 16 vertebrae, rather than the twelve noted by White (1970). Our examination of these vertebrae showed that, although the transverse processes are broken on all of the vertebrae, enough of their bases remain to show the presence of foramina in five of them similar to those found in modern *Coendou* but not in modern *Erethizon*. It is not possible to tell whether any of the transverse processes were fully bifurcated. It is difficult to estimate how many—if any—caudals are missing. Based on what is preserved, the number of caudal vertebrae indicates a tail length at the upper end of the range of *Erethizon*. The presence of the foramina in the transverse processes, on the other hand, suggests *Coendou*.

Thus, the fossil porcupines from western North American have few traits that permit a confident assignment to genus. The ages of the northern (Idaho) and southern (Vallecito Creek and El Casco) fossils are similar and are somewhat younger than the fossils from the San Timoteo Badlands and Arizona. It seems plausible to state that the fossils from Idaho, because of their northern latitude, suggest that a substantial evolutionary process had already occurred to allow survival during seasonal climate changes which included significant cooling not experienced by their Neotropical ancestors (Graham, 1999). Physical evidence to support that interpretation, however, is limited to a single fossil with an incisor procumbency as in modern *Erethizon* (noting also that the more southerly Florida fossils all have procumbency measurements in the range of modern *Coendou*). Square cross-sectional shapes of several incisors, both in Idaho and in California, add some weight to the evidence in support of *Erethizon*. On the other hand, the foramina in the transverse processes of the caudal vertebrae look like *Coendou*. Nevertheless, based on the scenario described below, we retain Frazier's (1981) assignment of the genus *Erethizon* to the Pliocene-Pleistocene fossils of the western United States, with the exception of the El Golfo fossils that we assign to *Coendou*.

Cumberland Cave

As with most of the North American fossil sites in which porcupines are found, determination of the age of the Cumberland Cave fossils is difficult and based only on biochronologic data. A generally recognized estimate suggests an age range of the fauna to be between 0.5 and 0.9 Ma (Bell et al., 2004). Cumberland Cave in Maryland and Port Kennedy Cave in Pennsylvania (with two isolated teeth) are about 250 miles in latitude south of the Idaho Grand View fauna but are the northernmost localities on the east coast of North America from which fossil porcupines are reported.

The erethizontids from Cumberland Cave ascribed by White (1970) to an evolutionary position intermediate between the immigrant *Coendou* and modern *Erethizon* were assigned unequivocally by Frazier (1981) to *Erethizon*, as he did with all the fossils from North America. According to Gidley and Gazin (1938), the faunal assemblage includes taxa associated with both colder and warmer environments, so not all taxa may have been contemporaneous. But it is also possible that the assemblage indicates a nonanalog fauna (Semken et al., 2010) rather than a time-averaged sample resulting from the mixing of taxa from different times. Our examination of the porcupines from Cumberland Cave (Table 5) supports White's (1970, p. 13) conclusions that the population is morphologically intermediate between *Coendou* and *Erethizon,* which better fits with the interpretation of a non-analog fauna.

The cheek-tooth alveolar lengths are all the size of modern *Erethizon* (n=8), with one exception: USNM V 25689 is the size of a large modern *Coendou*.

All five of the p4/m1 ratios are in the range of overlap.

Of four incisors associated with p4's, two have a shape as is found in modern *Erethizon* and two are elongated as in *Coendou*. Five incisors associated with dp4's or an unerupted p4 all have the expected square shape of a juvenile porcupine.

Eight cheek-tooth axes relative to the incisors are measurable. Seven are directed laterally and one (USNM V 7671, a juvenile) medially.

Five individual animals are measureable for angles of procumbency. Of three buccal angles, one (USNM V 8130) falls into the range known only for *Coendou* and two are in the area of overlap. Of four lingual angles, one (USNM V 8130) has a value as in *Coendou*, one is in the area of overlap, and two (USNM V 7670 and V 25689) are in the range for *Erethizon*.

To summarize, of the twelve dentaries from Cumberland Cave, six have single traits that are distinctive as to genus in modern animals. Two adults (USNM V 7672 and V 8128) have incisors like *Erethizon*; one adult (USNM V 25691) has an incisor as in *Coendou*; one juvenile (USNM V 7670) has an angle of incisor procumbency typical of *Erethizon* and one juvenile (USNM V 8130) has an angle typical of *Coendou*. USNM V 7671, a juvenile, has a cheek-tooth axis medial to the incisor. One adult dentary (USNM V 25689) has three distinctive traits: The length of its cheek-tooth row is as in modern *Coendou*, and its incisor is shaped as in *Coendou*, but it has an angle of incisor procumbency as found in modern *Erethizon*.

Explaining the mix of traits in these fossils seems to involve three possibilities. First, as Gidley and Gazin (1938) proposed, the fossils may represent different assemblages of animals from different times. Second, porcupines from the north and porcupines from the south intermingled at Cumberland Cave. Third, the fossils represent an intermediate stage of evolution in which Neotropical traits and cold-adaptive traits had a more evenly expressed presence in porcupine populations than that which is seen in modern *Erethizon*. Based on the absence in the fossils from Florida of traits found in *Erethizon* and on the scenario presented in the Discussion, where we suggest a southward migration of cold-adapted porcupines along the Appalachian Mountain corridor, the third alternative appears to more closely fit the admittedly sparse data and so we retain the assignment by Frazier (1981) of the fossil porcupines from Cumberland Cave to *Erethizon*.

Aguascalientes, Mexico

A single dentary (UMMP V-47106) recovered from the Cedazo Formation (Hibbard and Mooser, 1963) is intriguingly situated in central Mexico just north of modern *Coendou* populations and south of the range of modern *Erethizon* (Fig. 1). Dating of the material is problematic, with the latest estimate by Bell et al. (2004) of an age between 1.0 and 1.8 Ma. The fauna was thought by Frazier (1981) to be Rancholabrean. Our analysis shows the cheek-tooth row is slightly longer than the longest modern *Erethizon*; the p4/m1 ratio is in the area of overlap between modern *Erethizon* and *Coendou*; the incisor shape more closely fits *Coendou* but is at the top of the range of *Erethizon*; the cheek-tooth axis is directed lateral to the incisor; and the angle of incisor procumbency falls well within the range of *Coendou*, at the very top of the range for *Erethizon* (Table 4). The fossil was assigned to the genus *Coendou* by White (1968) and to the genus *Erethizon* by Frazier (1981).

Although diagnostic features that would permit definitive assignment of this fossil to either *Coendou* or *Erethizon* are lacking, we tentatively assign it to the genus *Coendou* on the basis of the shape of its incisor, the direction of the cheek-tooth axis, and the angle of incisor procumbency, all of which align more closely to *Coendou*. In addition, the location of the fossil near the northern extent of modern *Coendou* and at a much greater distance south of the known range of modern *Erethizon* is a secondary consideration that also supports the assignment to *Coendou*.

Fauna of the Rancholabrean NALMA

Erethizontid fossil dentaries associated with the fauna of the Rancholabrean NALMA include those from Shelter Cave, New Mexico (fossil age as in Thompson et al., 1980) discussed above; a single dentary of a very young animal from San Josecito Cave, Nuevo Leon, Mexico (age as in Arroyo-Cabrales et al., 1995), which has the *Erethizon* angle of incisor procumbency (buccal 126 degrees, lingual 129 degrees); and a dentary from Edisto Beach, South Carolina, which we did not examine but which appears in a published illustration (Sanders, 2002) to have the large p4 characteristic of *Erethizon*. With the possible exception of the Aguascalientes fossil, we are not aware of any published mention of porcupines other than *Erethizon* being present in the fauna of the Rancholabrean NALMA. We therefore accept the assignment by Frazier (1981) of porcupines in the fauna of the Ranchlabrean NALMA to the genus *Erethizon*.

SYSTEMATIC PALEONTOLOGY

Based on the modern and fossil descriptions above and on the following discussion, we propose this revision for the systematics of the erethizontids of North America. The generic names *Hystrix*, *Cercolabes*, *Sphingurus*, *Synoetheres*, *Synetheres*, *Coendu, Sphiggurus*, and *Echinoprocta* were all, at some point in the past, applied to various Neotropical porcupine species and are included here under the genus *Coendou*.

Order Rodentia Bowditch, 1821
Suborder Hystricomorpha Brandt, 1855
Family Erethizontidae Bonaparte, 1845
Genus *Coendou* Lacépède, 1799
Coendou poyeri (Hulbert, 1997)

Erethizon poyeri Hulbert, 1997:624, fig.1.

LOCALITIES AND MATERIAL EXAMINED. Haile 7C, Florida: UF 121740 (holotype), UF 121747 (measurements by Hulbert, 1997); Haile 7G.

Coendou kleini (Frazier, 1981) new combination

Erethizon kleini Frazier, 1981:43, figs. 8–11, 14–19.

LOCALITIES AND MATERIAL EXAMINED. Inglis 1A, Florida: UF 21473 (holotype), UF 21474, UF 21475.

Coendou cf. *C. kleini*

LOCALITIES AND MATERIAL EXAMINED. El Golfo de Santa Clara, Sonora, Mexico: AWC 10858, AWC 12197, AWC 12540, AWC 13592, AWC 14810, IGM 10199.

Coendou spp.

Erethizon dorsatum Frazier, 1981:44, figs. 5–11, 17; Morgan and White, 1995:421, fig. 5.

LOCALITIES AND MATERIAL EXAMINED. Haile 16A, Florida: UF 21490, UF 21492. Leisey 3A, Florida: UF 124632, UF 135669. Coleman 2A, Florida: UF 11776. Aguascalientes, Mexico: UMMP V-47106.

Erethizon Cuvier 1822
Erethizon bathygnathum (Wilson, 1935)

E. bathygnathum Wilson 1935:220.
Coendou stirtoni White 1968:2, figs. 1–3.
E. bathygnathum Shotwell 1970:12, 15–16, 71–72, fig. 34.
C. bathygnathum White 1970:7 (*bathygnathum* apparently misspelled *brachygnathum* by White).
E. bathygnathum Frazier 1981:40, figs 8–11, 14, 16–19.

LOCALITIES AND MATERIAL EXAMINED. Jackass Butte (Grandview fauna), Idaho: USNM 13684 (holotype), UO F-16271, UO F-16272; Vallecito Creek, California: IVCM 309, IVCM 460, ABDSP (LACM) 1563/V6136, LACM 61420, LACM 6210. Wolf Ranch, Arizona.

Erethizon cascoensis (Frazier, 1981)

Coendou cascoensis White 1970:3, figs. 1–2.
E. cascoensis Frazier 1981:42, figs. 5–7, 11.

LOCALITIES AND MATERIAL EXAMINED. El Casco, California: F:AM 17883-1, F:AM 17883-2, F:AM 17883-4, F:AM 17883-5, F:AM 17883-6.

Erethizon dorsatum (Cuvier, 1822)

Hystrix dorsata Linnaeus 1758.
E. dorsatum Cuvier 1822:413–484.
E. cloacinus Cope 1871:73–102.
E. godfreyi Allen 1904:383–384.
Coendou cumberlandicus White 1970:7.
E. dorsatum Frazier 1981:44, figs. 5–12, 14–19.

LOCALITIES AND MATERIAL EXAMINED. Cumberland Cave, Maryland: USNM V 7668, USNM V 7669, USNM V 7670, USNM V 7671, USNM V 7672, USNM V 7673, USNM V 8128, USNM V 8130, USNM V 8134, USNM V 25689, USNM V 25690, USNM V 25691; San Josecito Cave, Nuevo Leon, Mexico: LACM 2968; Shelter Cave, New Mexico: LACM 1748, LACM 150691, LACM 150692, LACM 150693, LACM 150694, LACM 150695, LACM 150696, LACM 150697, LACM uncatalogued; Port Kennedy Cave, Pennsylvania; Conard Fissure, Arkansas; Trout Cave, West Virginia; Apollo Beach, Florida; Port Charlotte, Florida; additionally, erethizontids of all North American localities of Rancholabrean fauna, excepting the Aguascalientes fossil, are retained in the taxon *Erethizon dorsatum*.

DISCUSSION

Hibbard and Mooser (1963), examining porcupine dentition, observed that *Erethizon dorsatum* "is probably one of the most variable rodents in North America." Our studies support that observation and extend it to other mandibular characteristics as well (e.g., length of diastema, superior–inferior depth of mandible, and the shapes of the ascending ramus and angular process). The Neotropical porcupines are similarly variable. As noted by Voss et al. (2013:28) with regard to modern *Coendou*, "most craniodental characters known to vary among Recent erethizontids are either autapomorphies ..., or they are so variable within species as to be effectively useless for phylogenetic analysis." Many of the same variable traits appear in both *Erethizon* and *Coendou*. This parallel variability and the accompanying close anatomical similarities of *Coendou* and *Erethizon* demonstrate the close kinship of the two taxa but also create difficulties in identifying anatomical features that can reliably distinguish them. Some of the traits we identified, such as the differing relative sizes of p4 versus m1 and the differing cross-sectional shapes of the incisor, are distinctive in extant populations but only in their more extreme values, with their variant morphologies possibly demonstrating phenotypic plasticity that has accumulated over evolutionary time. More complex changes, as in the shape of the mandible to accommodate the biting of bark, may reflect the influence of direct evolutionary change in the immigrant porcupines in response to a more strongly seasonal environment with the resultant changes in food supply and so might not be expected to be seen in the Neotropical porcupines.

Due to the extensive variability present in these animals, we have found that using morphologic differences in modern animals to identify genera of fossil animals presents significant possibilities for error. The variability means that a single trait in a single fossil often cannot be used to identify a porcupine beyond Erethizontidae, and, because the number of fossils are sparse in individual localities and the fossil sites are separated by long distances in space and in time, any attempt to identify genera and species of the fossils and assemble a reasonable narrative of their history inevitably leads to speculation. Nevertheless, we can only evaluate the fossil material that is available to us and base our conclusions on that information.

With these caveats and with the acknowledgement that future fossil finds may alter our conclusions, we posit that there are reasonable alternatives to the presently accepted scenario for North American porcupines.

We disagree with Frazier's statement (1981:47) that "The fossil record shows no major structural changes from the three early fossil forms to the living species." The mandibular differences we describe above are significant and reflect in modern *Erethizon* an evolutionary response to the new environment the immigrants had entered. There is no indication of these changes in the early porcupines from Florida, despite a geological record covering about 1 Ma. The first fossil record in eastern North America of *Erethizon*-like mandibular changes that we found occurs at Cumberland Cave in Maryland, whose fossils are of an uncertain age but are probably less than 1 Ma.

We propose that, if the closure of the Isthmus of Panama did take place over a protracted period of time, beginning in the middle Miocene or earlier (Bacon et al., 2015; Montes et al., 2015), the tectonic events occurring then may have provided the extant species multiple opportunities for vicariant episodes. During that time, it appears that the Neotropical and North American erethizontid lineages did begin to diverge, according to the research of Vilela et al. (2009) and Voss et al. (2013). Lacking fossils from that extended period of time, we can only state that at present there are no fossils referable to *Erethizon* in either South or Central America, with the entire fossil record of the genus being confined to North America. It appears that at least the morphological evolution of features of the skeleton that define *Erethizon* occurred in North America.

Once the isthmus had formed, erethizontids were able to begin moving northward into North America. With the large gap in the fossil record, the exact time of the initial and possible subsequent dispersal episodes cannot be known, but at some point during the move north, possibly in central or northern Mexico, a single migratory pathway from the south split into two pathways, one following the Gulf of Mexico and terminating in Florida, the other continuing north into what is now California and the northwestern United States and eventually even farther north into Canada. At a relatively early time, the western pathway lost contact with the stem and eastern pathways. Evolutionary changes occurred in the western animals that allowed them to withstand and even thrive in the increasingly seasonally cold environments. As the western group of porcupines evolved this substantial ability to survive what became Ice Age conditions, they spread over the northern latitudes of North America, moving east as well as north. At the eastern extent of their movement, the Appalachian Mountains provided a pathway to move south. The Cumberland Cave fossils, with their mix of traits, may provide a snapshot of the evolutionary transition between the original immigrants and today's *Erethizon*.

The porcupines in the Gulf of Mexico migratory branch may have thrived for as long as a million years. Based on the age of the porcupines from El Golfo assigned to *Coendou* (*ca.* 1 Ma) and the estimated age of the fossils from Cumberland Cave assigned to *Erethizon* (0.5–0.9 Ma), we suggest that at about 1 Ma, for reasons possibly related to the effects of Ice Age conditions, the connection between the southeastern porcupines and their southern subtropical relatives became attenuated and then severed. Now isolated, the Florida porcupines did not evolve traits that allowed them to continue and eventually became extinct.

SUMMARY

A morphological study of modern Neotropical (*Coendou* spp.) and North American (*Erethizon dorsatum*) erethizontid dentaries and caudal vertebrae has found physical differences that distinguish the two genera. Application of these findings to the fossil porcupines from Shelter Cave in North America and those from Lagoa Santa in Brazil supports our contention that a genus cannot be identified based solely on size. Consequently, we propose the following taxonomic revision of North American erethizontids. All fossils from Florida that are older than the Rancholabrean North American LMA plus a single fossil from Aguascalientes, Mexico, are reassigned from *Erethizon* to *Coendou*. In addition, erethizontid fossils from El Golfo de Santa Clara, Sonora, Mexico, described in this paper, are assigned to *Coendou*. The remaining North American erethizontid fossils are retained in *Erethizon*, as in Frazier (1981).

We present a theoretical migratory pathway into North America from tropical America for the erethizontids that dispersed via the Panamanian land bridge (erethizontids that we consider morphologically to have been *Coendou*). At some point in central to northern Mexico, a single northerly pathway divided into two, with the western branch continuing north into northwestern North America before then turning east at higher latitudes. This branch adapted to the cold-weather conditions it encountered and evolved into a new genus: *Erethizon*. The eastern branch of the Mexican population dispersed east and followed the southern coast of North America into Florida. These Neotropical porcupines retained the traits of their immigrant ancestors and ultimately became extinct.

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Table 1 Dentary measurements of modern North American *Erethizon dorsatum* and modern Neotropical *Coendou* species. Data entries, in order, are means, ranges, standard deviations, and numbers of individuals measured. Measurements are in millimeters or degrees.

	E. dorsatum	*C. bicolor*	*C. mexicanus*	*C. nycthemera*	*C. prehensilis*	*C. rufescens*
Length cheek-tooth row						
Mean ± SD	28.6 ± 1.6	21.5 ± 1.2	22.0 ± 1.2	16.4 ± 0.7	21.8 ± 2.0	18.7 ± 1.1
Range	25.4–30.9	19.6–23.1	19.3–24.3	15.1–17.6	17.9–25.7	17.2–20.6
n	72	10	23	7	33	12
Length, width p4						
Mean ± SD	7.9 ± 0.6, 6.7 ± 0.5	5.7 ± 0.5, 4.7 ± 0.8	5.8 ± 0.3, 4.6 ± 0.3	4.1 ± 0.4, 3.6 ± 0.4	5.4 ± 0.5, 4.6 ± 0.5	4.6 ± 0.5, 4.1 ± 0.2
Range	6.6–9.1, 5.7–7.8	5.4–6.1, 4.0–5.1	5.4–6.3, 4.1–5.3	3.3–4.5, 2.9–3.9	4.5–6.6, 3.7–5.4	3.7–5.0, 3.7–4.4
n	41	6	17	7	29	8
Length × width p4						
Mean ± SD	52.9 ± 6.6	26.5 ± 5.4	26.6 ± 2.3	14.8 ± 2.6	25.0 ± 4.3	18.8 ± 2.4
Range	41.6–67.3	22.4–29.9	22.1–29.7	9.6–16.8	16.7–32.3	14.4–22.0
n	41	6	17	7	29	8
Length, width dp4						
Mean ± SD	7.3 ± 0.5, 5.4 ± 0.3	4.7 ± 0.7, 3.5 ± 0.5	5.0 ± 0.4, 3.7 ± 0.4		4.9 ± 0.4, 4.0 ± 0.3	4.5 ± 0.0, 3.4 ± 0.1
Range	5.9–7.7, 4.5–6.0	4.2–5.5, 3.0–3.9	4.4–5.3, 3.5–3.9	3.9, 2.7	4.3–5.2, 3.1–4.5	4.5–4.5, 3.3–3.5
n	37	3	6	1	11	4
Length × width dp4						
Mean ± SD	39.1 ± 3.7	16.6 ± 4.4	18.5 ± 2.7		19.6 ± 2.8	15.4 ± 0.4
Range	26.6–42.4	12.6–21.5	17.2–19.6	10.5	13.3–23.4	14.9–15.8
n	37	3	6	1	11	4
Length, width m1						
Mean ± SD	6.4 ± 0.3, 6.2 ± 0.3	4.9 ± 0.6, 4.7 ± 0.6	5.1 ± 0.4, 4.6 ± 0.3	3.9 ± 0.4, 3.7 ± 0.4	5.2 ± 0.5, 4.7 ± 0.4	4.2 ± 0.3, 4.0 ± 0.4
Range	5.9–7.1, 5.6–6.9	4.4–5.4, 4.0–4.9	4.5–5.8, 3.4–5.4	3.3–4.3, 2.8–4.0	4.3–6.2, 3.7–5.4	3.7–4.8, 3.5–4.8
n	76	8	26	8	36	12
Length × width m1						
Mean ± SD	40.1 ± 3.1	23.1 ± 4.9	23.4 ± 2.8	14.6 ± 2.7	24.3 ± 4.2	16.7 ± 2.5
Range	34.2–47.6	18.0–27.5	15.5–30.2	9.2–17.2	16.7–30.2	13.0–23.0
n	76	8	26	8	36	12
Length × width p4/length × width m1						
Mean ± SD	1.3 ± 0.2	1.2 ± 0.1	1.1 ± 0.1	1.0 ± 0.1	1.0 ± 0.1	1.1 ± 0.1
Range	1.1–1.8	1.1–1.3	0.8–1.4	0.9–1.10	0.8–1.2	1.0–1.2
n	40	4	19	7	8	8
Length, width m2						
Mean ± SD	6.4 ± 0.4, 6.5 ± 0.4	5.1 ± 0.5, 4.8 ± 0.7	5.0 ± 0.4, 4.8 ± 0.4	4.0 ± 0.5, 3.6 ± 0.4	5.1 ± 0.5, 5.0 ± 0.4	4.4 ± 0.3, 4.1 ± 0.4
Range	5.4–7.2, 5.7–7.3	4.4–5.5, 4.3–5.1	4.3–5.5, 3.4–5.5	3.2–4.5, 2.6–4.0	4.1–6.0, 4.2–6.0	3.9–4.8, 3.7–4.5
n	73	9	23	8	31	12
Length × width m2						
Mean ± SD	41.5 ± 4.0	24.5 ± 5.2	23.6 ± 3.6	14.3 ± 2.8	25.8 ± 4.5	18.1 ± 2.6
Range	34.0–51.1	18.9–26.0	13.9–29.7	8.3–17.6	17.2–33.6	13.8–21.6
n	73	9	23	8	31	12
Length, width m3						
Mean ± SD	6.8 ± 0.4, 6.3 ± 0.4	5.2 ± 0.7, 4.5 ± 0.8	4.9 ± 0.4, 4.6 ± 0.5	4.0 ± 0.4, 3.4 ± 0.6	5.2 ± 0.6, 4.6 ± 0.4	4.4 ± 0.4, 3.8 ± 0.4
Range	6.0–7.8, 5.5–7.2	4.7–5.6, 3.9–5.1	3.9–5.7, 3.0–5.2	2.8–4.4, 2.6–3.6	4.1–6.5, 4.0–5.4	3.7–5.0, 3.1–4.3
n	65	6	22	6	30	10
Length × width m3						
Mean ± SD	43.3 ± 3.8	23.4 ± 6.3	22.7 ± 3.5	13.5 ± 3.1	23.3 ± 6.1	16.9 ± 2.7
Range	35.4–51.8	18.3–17.5	11.7 –28.1	7.3–15.5	16.8–32.8	12.6–21.5
n	65	6	22	6	30	10
A-P diam., width incisor*						
Mean ± SD	4.7 ± 0.5, 4.7 ± 0.5	3.9 ± 0.4, 3.0 ± 0.4	4.1 ± 0.6, 3.1 ± 0.4	3.0 ± 0.4, 2.4 ± 0.3	4.3 ± 1.0, 3.3 ± 0.7	3.3 ± 0.5, 2.9 ± 0.5
Range	4.2–5.3, 3.9–5.4	3.7–4.1, 2.8–3.3	3.7–4.6, 2.7–3.5	2.3–3.7, 1.8–2.7	3.0–5.3, 2.5–3.9	2.7–3.5, 2.2–3.5
n	38	5	18	6	27	8

Table 1 Continued.

	E. dorsatum	*C. bicolor*	*C. mexicanus*	*C. nycthemera*	*C. prehensilis*	*C. rufescens*
A-P diam./width incisor*						
Mean ± SD	1.0 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	1.1 ± 0.1
Range	0.9–1.2	1.2–1.4	1.1–1.5	1.2–1.4	1.2–1.4	1.0–1.3
n	38	5	18	6	27	8
Length of diastema*						
Mean ± SD	16.7 ± 3.0	12.7 ± 2.2	13.1 ± 2.1	8.4 ± 1.7	12.0 ± 3.1	10.1 ± 1.9
Range	11.7–22.3	10.8–14.9	11.3–15.7	6.2–10.1	7.7–16.4	7.6–13.1
n	39	7	19	7	29	8
Length diastema/length cheek-tooth row*						
Mean ± SD	0.57 ± 0.08	0.59 ± 0.08	0.59 ± 0.08	0.49 ±	0.48 ± 0.09	0.54 ± 0.09
Range	0.41–0.74	0.49–0.69	0.49–0.77	0.38–0.62	0.41–0.74	0.44–0.68
n	39	7	19	7	28	8
Length diastema/length cheek-tooth row**						
Mean ± SD	0.50 ± 0.10	0.46	0.48 ± 0.05		0.51 ± 0.07	0.51 ± 0.15
Range	0.37–0.66	0.44, 0.48	0.44–0.55	0.32	0.41–0.57	0.39–0.73
n	26	2	4	1	4	4
Length of symphysis*						
Mean ± SD	32.8 ± 3.7	25.2 ± 2.7	24.8 ± 2.7	18.0 ± 1.9	25.3 ± 5.0	21.4 ± 2.2
Range	27.5–38.9	24.0–26.9	20.0–28.6	15.9–20.4	18.5–30.6	19.0–23.6
n	40	7	18	7	29	8
Angle of incisor procumbency: buccal, lingual						
Mean ± SD	127 ± 3.4, 133 ± 2.8	135 ± 3.7, 139 ± 3.3	133 ± 3.2, 140 ± 2.3	133, 139	135 ± 2.4, 141 ± 0.8	133 ± 4.8, 139 ± 3.7
Range	121–134, 126–138	132–142, 135–145	128–138, 137–144	132–135	130–142, 134–143	130–143, 132–144
n	42, 19	7, 7	12, 8	3, 1	24, 8	8, 7
Cheek-tooth row axis relative to incisor. Numbers of individuals: lateral, centered, medial	40, 9, 9	10, 0, 0	22, 0, 0	0, 0	36, 0, 0	7, 1, 0

*Adults, defined as having a p4.

**Subadults, defined as having a dp4 and an erupted m3.

Table 2 Dentary measurements of fossil erethizontids from El Golfo de Santa Clara, Sonora, Mexico. Measurements are in millimeters or degrees.

	AWC 10858	**AWC 12197**	**AWC 13592**	**AWC 14810**	**IGM 10199**
Length cheek-tooth row	25.8	25.4			
Length, width p4		5.6, 7.3			
Length × width p4		40.9			
Length, width m1			5.9, 6.6	5.6, 5.9	
Length × width m1			38.9	33.0	
Length × width p4/length × width					
Length, width m2	5.7, 6.0			5.9, 6.0	
Length × width m2	34.2			35.4	
Length, width m3	6.0, 5.2			6.0, 5.3	
Length × width m3	31.2			31.8	
A-P diam., width incisor	5.2, 4.7	5.3, 4.3		4.8, 4.3	5.4, 4.5
A-P diam./width incisor	1.1	1.2		1.1	1.2
Length of diastema		16.9			
Length of diastema/length of cheek-tooth row		0.67			
Length of symphysis		30.1			
Angle of incisor procumbency degrees; buccal/lingual	134/-			135/137	
Axis of cheek-tooth row relative to incisor	Lateral	Lateral			

Table 3 Dentary measurements of fossil erethizontids from Florida. Measurements are in millimeters or degrees.

	UF 121740 Haile 7C	**UF 121747 Haile 7C***	**UF 21473 Inglis 1A**	**UF 21474 Inglis 1A**	**UF 21475 Inglis 1A**	**UF 21490 Haile 16A**	**UF 21492 Haile 16A**	**UF 124632 Leisey 3A**	**UF 11776 Coleman 2A**
Length cheek-tooth row	32.7		26.5	25.6		30.0		31.3	
Length, width p4	7.5, 5.9	7.1, 5.4	7.1, 5.3	6.2, 5.4		8.1, 7.1		8.8, 6.5	
Length × width p4	44.3	38.3	37.6	33.5		57.5		57.2	
Length, width m1	7.4, 6.2		5.9, 5.3	5.5, 5.1	5.8, 5.3	6.6, 6.5	6.8, 6.2	7.4, 6.0	
Length × width m1	45.9		31.3	28.1	30.7	42.9	42.2	44.4	
Length × width p4/length × width m1	0.96		1.20	1.19		1.34		1.29	
Length, width m2	7.9, 6.7		6.0, 5.6	6.0, 5.7	6.0, 5.9	7.0, 7.0	7.1, 6.7	7.0, 6.4	
Length × width m2	52.9		33.6	34.2	35.4	49.0	47.6	44.8	
Length, width m3	6.5, 5.9		6.0, 4.8		5.3, 5.0	7.0, 6.6			6.7, 6.1
Length × width m3	38.4		28.8		26.5	46.2			40.9
A-P diam., width incisor	5.2, 4.5		4.7, 4.3			5.7, 5.3			
A-P diam./width incisor	1.2		1.1			1.1			
Length of diastema			15.8						
Length of diastema/length of cheek-tooth row			0.6						
Length of symphysis			29.7						
Angle of incisor procumbency; buccal/lingual			139/—	—/139		136/145		136/145	
Axis of cheek-tooth row relative to incisor (lateral, medial)	Lateral		Lateral	Lateral		Lateral		Lateral	

*dp 4; measurements from Hulbert, 1997.

Table 4 Dentary measurements of fossil erethizontids from Jackass Butte (USNM) and Grand View, Idaho (UO); El Casco, California (F:AM); Vallecito Creek, California (IVCM, LACM); and Aguascalientes, Mexico (UMMP). Measurements are in millimeters or degrees.

	USNM 13684	UO F-16271	UO F-16272	F:AM 17883-1	F:AM 17883-2	F:AM 17883-4	F:AM 17883-5	F:AM 17883-6	IVCM 309	IVCM 460	ABDSP(LACM) 1563/V6136	LACM 61420	LACM 6210	UMMP V-47106
Length -cheek-tooth row	34.2	33.6		30.1								31.3		31.1
Length, width p4	8.6, 7.8	8.4, 7.0				7.6, 6.5								9.0, 6.8
Length × width p4	67.1	58.8				49.4								61.2
Length, width m1	7.3, 7.0	7.7, 6.9	7.3, 7.3						7.2, 6.7					7.2, 6.8
Length × width m1	51.1	53.1	53.3						48.2					49.0
Length × width p4/length × width m1	1.31	1.11												1.25
Length, width m2	7.2, 7.1	7.8, 7.2	6.7, 7.5		6.9, 6.2				7.0, 7.7					7.3, 7.1
Length × width m2	51.1	56.2	50.3		42.8				53.9					51.8
Length, width m3		7.3, 6.7			6.6, 6.0				7.8, 7.0					7.2, 6.9
Length × width m3		48.9			39.6				54.6					49.7
A-P diam., width incisor	7.3, 6.4	6.4, 5.7	5.2, 5.3	5.7, 5.5			5.4, 4.9	5.1, 5.0		5.7, 5.7				5.7, 4.6
A-P diam./width incisor	1.1	1.1	1.0	1.0			1.1	1.0		1.0				1.2
Length of diastema			11.2	23.3										15.0
Length of diastema/length of cheek-tooth row				0.8										0.48
Length of symphysis		37.1		40.1										32.3
Angle of incisor procumbency; buccal/lingual		-/131												134/136
Axis of cheek-tooth row relative to incisor (lateral, medial)	Lateral	Lateral		Lateral										Lateral

Table 5 Dentary measurements of fossil erethizontids from Cumberland Cave, Maryland. Measurements are in millimeters or degrees.

	USNM V 7668	USNM V 7669	USNM V 7670*	USNM V 7671*	USNM V 7672	USNM V 7673*	USNM V 8128	USNM V 8130*	USNM V 8134*	USNM V 25689	USNM V 25690*	USNM V 25691
Length cheek-tooth row			26.7	28.9	29.7		28.5	27.6	28.1	24.5	28.4	28.4
Length, width p4	7.5, 6.4		6.1, 4.4	6.0, 4.9	7.8, 6.3	6.2, 5.3	7.5, 6.6	6.2, 4.5	6.5, 4.5	7.0, 6.1	7.6, 4.8	7.8, 6.6
Length × width p4	48.0		26.8	29.4	49.1	32.9	49.5	27.9		42.7	36.5	51.5
Length, width m1	6.7, 6.1	6.6, 6.4	6.3, 5.6	6.8, 5. 5	6.5, 6.3	6.5, 6.5		6.0, 5.8	6.1, 5.7	6.0, 5.8	6.2, 5.2	6.6, 6.2
Length × width m1	40.9	42.2	35.3	37.4	41.0	42.3		34.8	34.8	34.8	32.2	40.9
Length × width p4/length × width m1	1.17				1.20					1.23	1.13	1.26
Length, width m2	6.5, 6.4	6.2, 6.5	6.4, 6.2	7.0, 6.3	6.9, 6.4	6.2, 6.2	6.4, 6.2	6.2, 6.1	6.2, 6.0	6.1, 5.9	6.2, 5.7	6.5, 6.1
Length × width m2	41.6	40.3	39.7	44.1	44.2	38.4	39.7	37.8	37.2	36.0	35.3	39.7
Length, width m3		6.1, 6.4	6.5, 5.9	6.6, 5.6	6.2, 6.4		6.0, 5.8	6.7, 5.8	6.5, 6.0		6.1, 5.9	
Length × width m3		39.0	38.4	37.0	39.7		34.8	38.9	39.0		36.0	
A-P diam., width incisor			4.4, 4.6	4.6, 4.7	5.3, 6.0		5.8, 5.7	4.7, 4.3	4.5, 4.0	5.7, 4.4	4.7, 4.9	5.6, 4.2
A-P diam./width incisor			1.0	1.0	0.9		1.0	1.1	1.1	1.3	1.0	1.3
Length of diastema				12.7				13.4		15.7		
Length of diastema/length of cheek-tooth row				0.4				0.5		0.6		
Length of symphysis			26.6	29.8			31.1	29.7		34.1		
Angle of incisor procumbency: buccal/lingual			—/130	Reconstructed			130/136	138/139	Incisor repaired	—/132	130/—	
Axis of cheek-tooth row relative to incisor (lateral, medial)		Lateral	Lateral	Medial	Lateral			Lateral	Lateral	Lateral	Lateral	

*Specimens are subadults; therefore measurements labelled p4 are dp4's.

Table 6 List of dentary traits that distinguish modern *Erethizon* and *Coendou*.

1. Length of cheek-tooth row	*Erethizon* > *Coendou*
2. Ratio of size of p4 to m1	*Coendou* < 1.10; *Erethizon* > 1.36
3. A-P diam./width of adult incisors	*Coendou* > 1.2 > *Erethizon*
4. Orientation of cheek-tooth row to incisor	*Coendou* lateral *Erethizon* 2/3 lateral, 1/3 medial
5. Angle of incisor procumbency (mean, range)	
Buccal	*Coendou* 134°, 128°–143° *Erethizon* 127°, 121°–134°
Lingual	*Coendou* 140°, 132°–145° *Erethizon* 133°, 126°–138°

Table 7 Dentary measurements of fossil erethizontids from Shelter Cave, New Mexico and Lagoa Santa, Brazil. Measurements are in millimeters or degrees.

	Shelter Cave	Lagoa Santa
Length cheek-tooth row		
Mean ± SD	29.2 ± 1.3	32.1 ± 1.7
Range	27.5–31.4	29.1–33.8
n	8	8
Length, width p4		
Mean ± SD		7.7 ± 0.4, 6.6 ± 0.4
Range	6.5, 6.8	7.3–8.3, 6.0–7.0
n	1	5
Length × width p4		
Mean ± SD		51.3 ± 4.9
Range	44.2	45.0–58.1
n	1	5
Length, width dp4		
Mean ± SD	None	5.4, 6.7
Range		7.0, 6.3; 5.6, 5.1
n		2
Length × width dp4		
Mean ± SD	None	36.2
Range		39.2, 32.1
n		2
Length, width ml		
Mean ± SD	5.8, 6.2	7.0 ± 0.4, 6.5 ± 0.3
Range	5.8, 5.8; 6.0, 6.3	6.4–7.4, 6.1–7.0
n	2	10
Length × width m1		
Mean ± SD	35.7	45.1 ± 3.8
Range	33.6, 37.8	39.0–51.8
n	2	10
Length × width p4/length × width m1		
Mean ± SD		1.08 ± 0.1
Range	1.31	1.00–1.20
n	1	5
Length, width m2		
Mean ± SD	6.3, 6.7	7.3 ± 0.5, 6.9 ± 0.2
Range	5.9–6.7; 6.7–6.7	6.6–8.5, 6.7–7.2
n	2	10
Length × width m2		
Mean ± SD	42.2	50.0 ± 4.6
Range	39.5–44.9	44.88–61.2
n	2	10
Length, width m3		
Mean ± SD	None	7.3 ± 0.3, 6.6 ± 0.3
Range		6.9–7.8, 6.2–7.1
n		7
Length × width m3		
Mean ± SD	None	48.0 ± 4.2
Range		42.8–55.4
n		7
A-P diam., width incisor*		
Mean ± SD	4.7 ± 0.3, 4.7 ± 0.2	5.7, 4.7
Range	4.0–5.3, 4.4–4.9	5.0–7.6, 4.1–6.3
n	5	3
A-P diam./width incisor*		
Mean ± SD	1.0 ± 0.1	1.2
Range	0.9–1.2	1.2–1.3
n	5	3
Length of diastema*		
Mean ± SD		20.9
Range	14.4	16.8–24.2
n	1	3
Length of diastema/length of cheek-tooth row–adults*		
Mean ± SD		0.63
Range	0.52	0.50–0.72
N	1	3
Length of diastema/length of cheek-tooth row–subadults**		
Mean ± SD	None	0.44
Range		0.41–0.46
n		2
Length of symphysis*		
Mean ± SD	29.6	37.2
Range	29.2–30.0	32.9–40.5
n	2	3
Angle of incisor procumbency, buccal, in degrees		
Mean ± SD	None	136
Range		134–138
n		3
Angle of incisor procumbency, lingual, in degrees		
Mean ± SD	126 ± 4.0	142 ± 1.4
Range	122–130	141–144
N	5	5
Axis of cheek-tooth row relative to incisor		
Numbers of individuals: medial, central, lateral	0, 2, 3	0, 0, 6

*Adults, defined as having a p4.

**Subadults, defined as having a dp4 and an erupted m3.

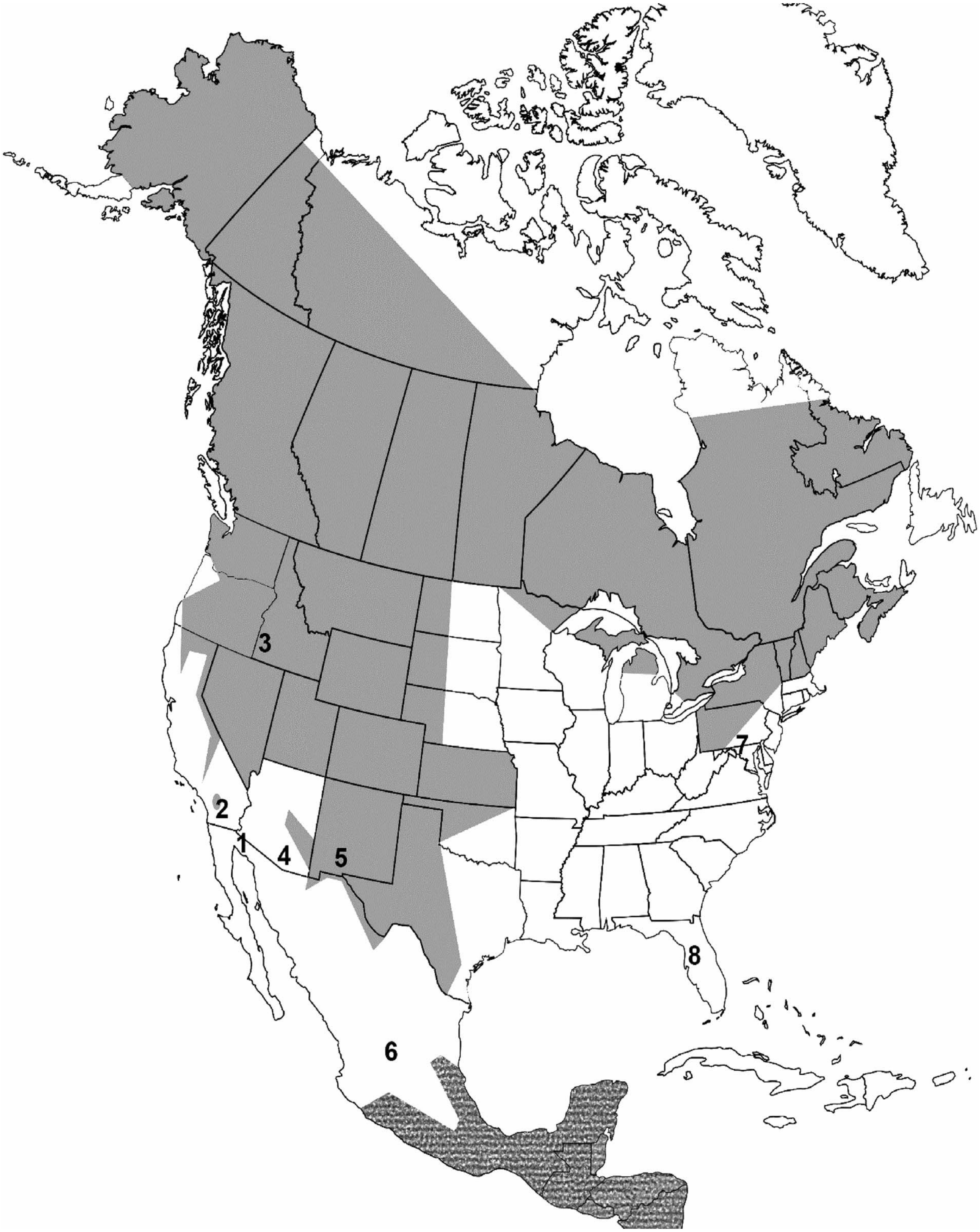

Figure 1 North American map showing distribution of modern *Erethizon dorsatum* (smooth) (Roze and Ilse, 2003) and *Coendou* spp. (stippled) (modified from Eisenberg and Redford, 1999). Fossil erethizontid localities are identified by number. Rancholabrean/Holocene localities are not shown, except for Shelter Cave. **1.** El Golfo de Santa Clara; **2.** Vallecito Creek, El Casco, San Timoteo; **3.** Jackass Butte (Grand View); **4.** Wolf Ranch; **5.** Shelter Cave; **6.** Aguascalientes (Cedazo); **7.** Cumberland Cave; **8.** Haile 7C, Inglis 1A, Haile 16A, Leisey 3A (clustered along the central Gulf Coast side of the Florida peninsula), Coleman 2A (inland east of the above).

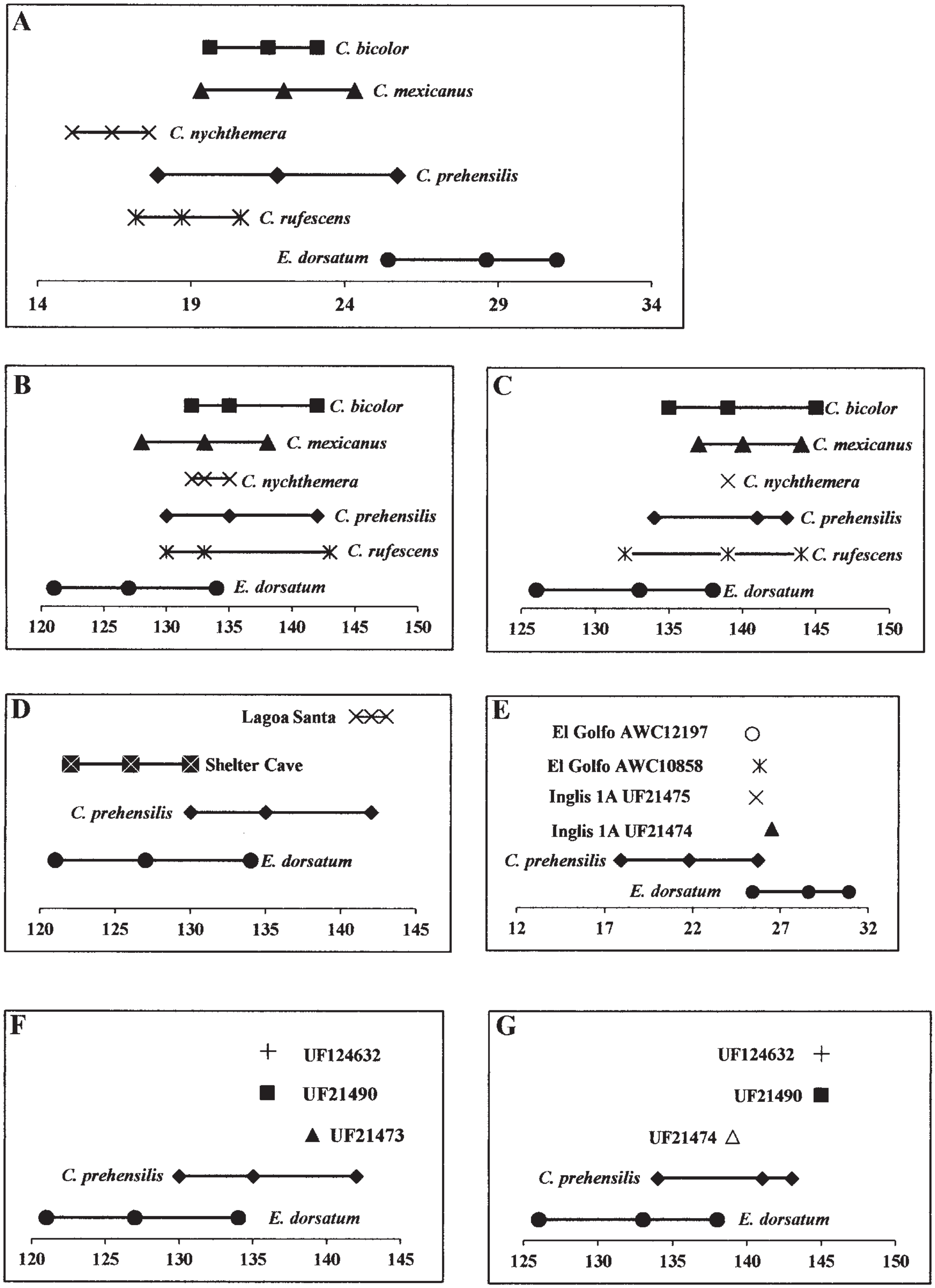

Figure 2 **A.** Shortest, mean, and longest lengths in millimeters of cheek-tooth rows for modern *Erethizon dorsatum* and five species of modern *Coendou*; **B.** lowest, mean, and highest buccal angles in degrees of incisor procumbency for modern *Erethizon dorsatum* and five species of modern *Coendou*; **C.** lowest, mean, and highest lingual angles in degrees of incisor procumbency for modern *Erethizon dorsatum* and five species of modern *Coendou*; **D.** lowest, mean, and highest buccal angles of incisor procumbency of *Erethizon dorsatum* fossils from Shelter Cave, New Mexico, and *Coendou magnus* fossils from Lagoa Santa, Brazil, compared with modern *E. dorsatum* and *C. prehensilis*, in degrees; **E.** comparison of lengths of cheek-tooth rows between modern *Coendou prehensilis*, modern *Erethizon dorsatum*, and fossil dentaries of *C. kleini* from Inglis 1A in Florida and *Coendou* cf. *C. kleini* from El Golfo in Sonora, in millimeters; **F.** comparison of buccal incisor procumbency between modern *Coendou prehensilis*, modern *Erethizon dorsatum*, and fossil Florida dentaries, in degrees; **G.** comparison of lingual incisor procumbency between modern *Coendou prehensilis*, modern *Erethizon dorsatum*, and fossil Florida dentaries, in degrees.

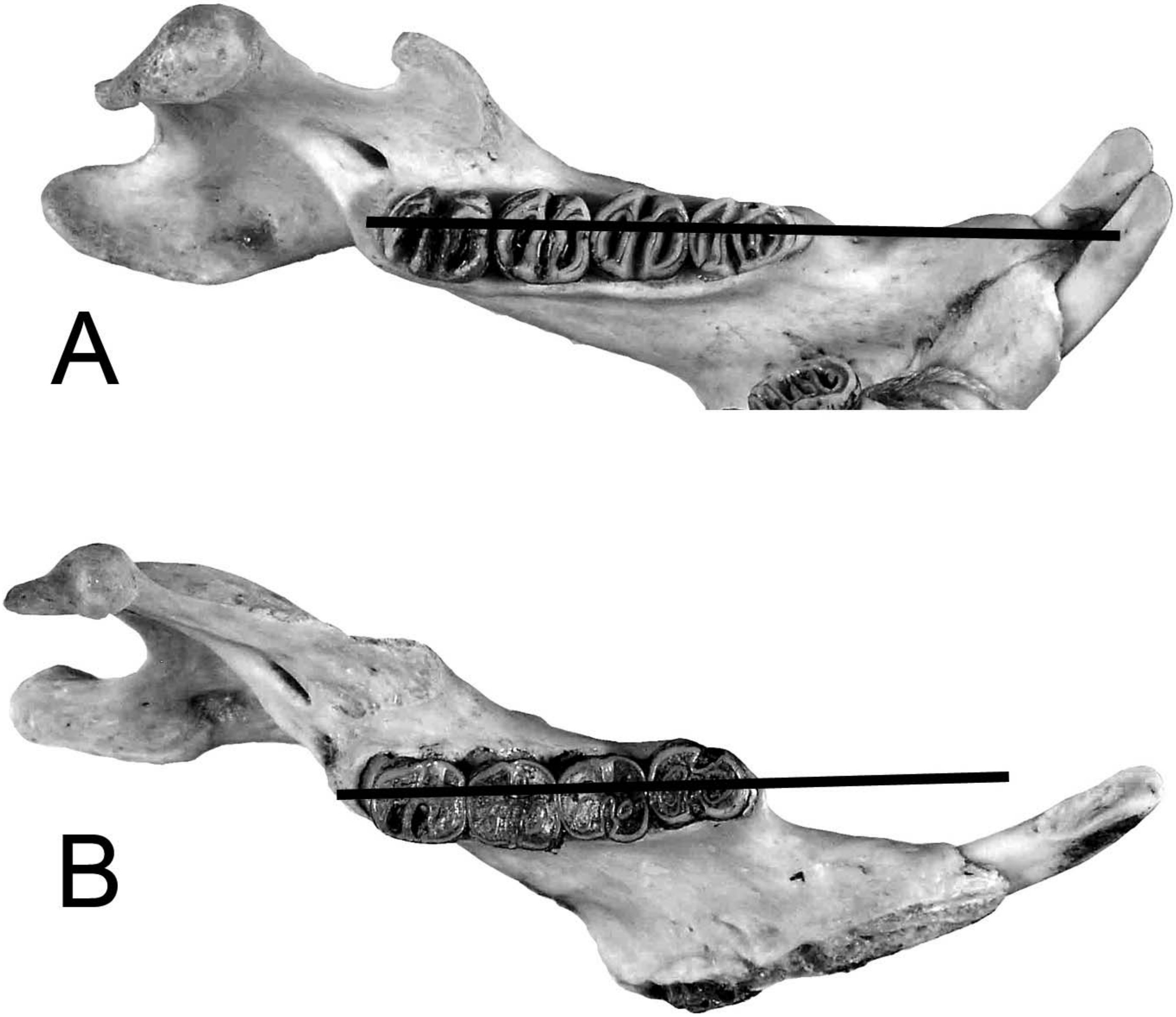

Figure 3 Occlusal views, left dentaries, of **A.** modern *Erethizon dorsatum* (AMNH 122664) and **B.** *Coendou mexicanus* (AMNH 123272), demonstrating method for measuring cheek-tooth axes relative to incisors and differences in axis direction between the two genera.

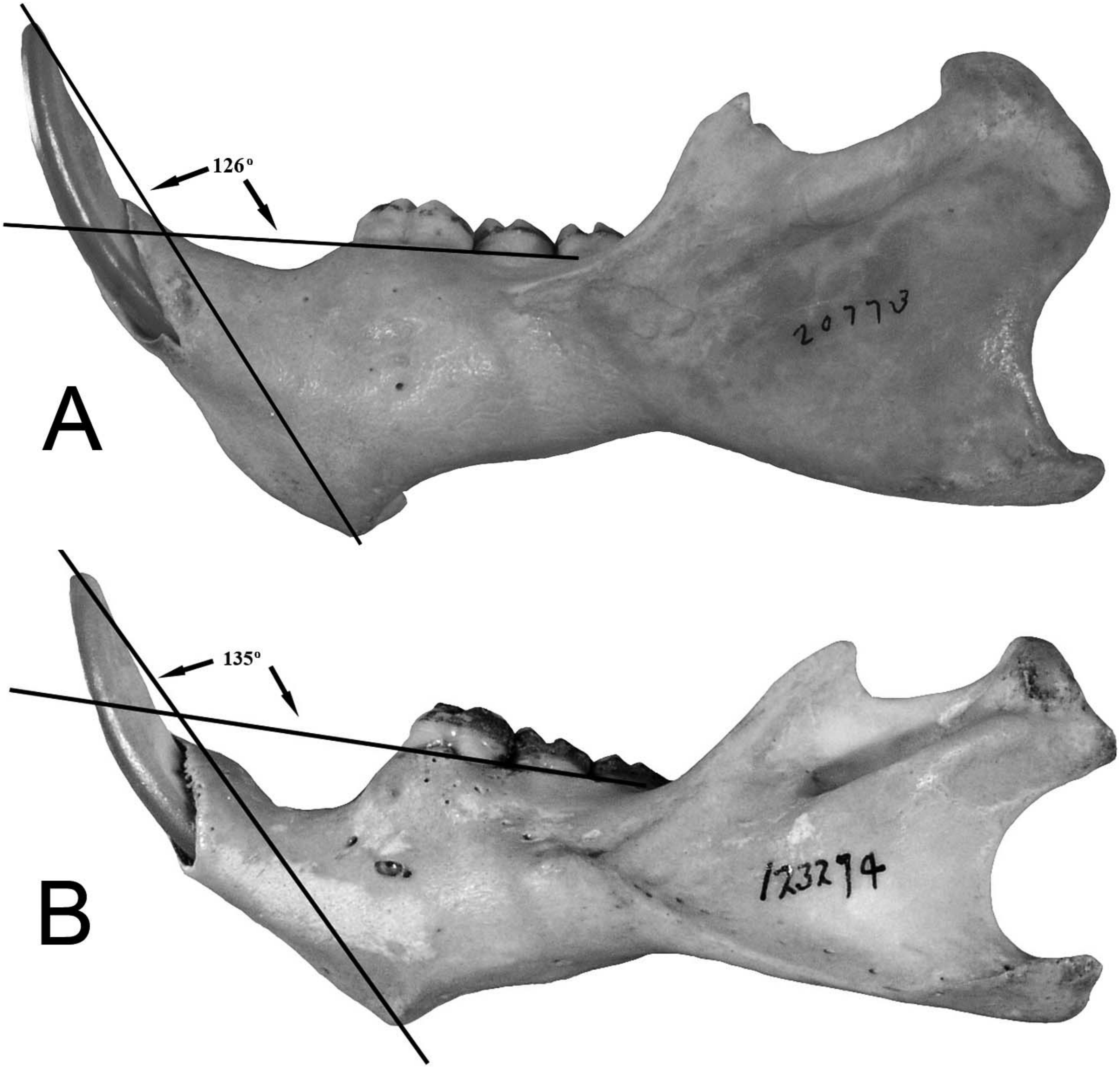

Figure 4 Buccal views, left dentaries., of **A.** modern *Erethizon dorsatum* (AMNH 20773) and **B.** *Coendou mexicanus* (AMNH 123274), demonstrating method for measuring incisor angle of procumbency.

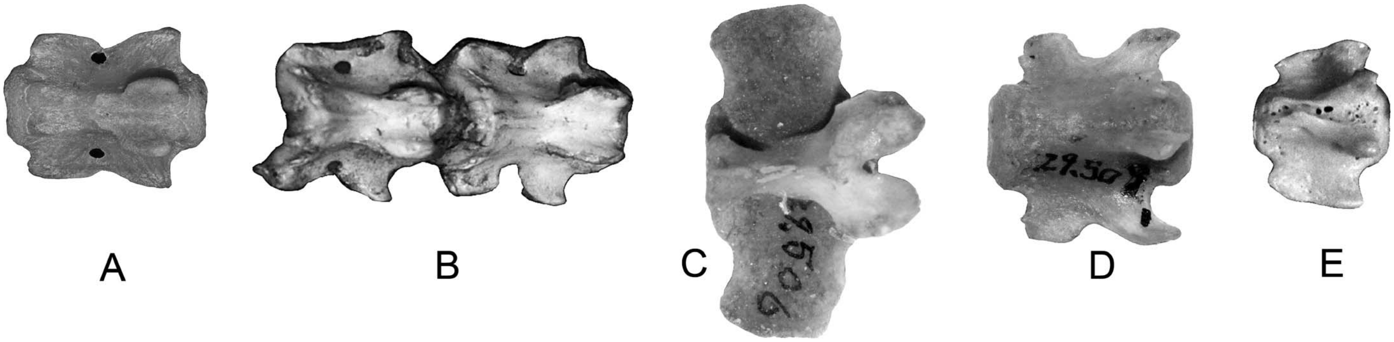

Figure 5 Examples of modern *Coendou* and *Erethizon* caudal vertebrae, demonstrating various anatomical states of the transverse processes. **A.** C14 from *C. prehensilis* (AWC 2) showing foramina and indentations in transverse processes; **B.** C16–17 from *C. prehensilis* (MNHN A2859) with foramina and bifurcated transverse processes; **C.** C8 from *E. dorsatum* (MNA Z9.506) lacking foramina and bifurcated transverse processes; **D.** C9 from *E. dorsatum* (MNA Z9.509) with bifurcated transverse processes; **E.** C9 from *E. dorsatum* (AWC 1) near end of tail, lacking foramina and bifurcated transverse processes.

Figure 6 Caudal vertebrae C19–24 from fossil *C. magnus* (Lagoa Santa, Brazil) (ZMUC, E Museo Lundil plate v Nr. 5 and 6), demonstrating foramina and bifurcated transverse processes as in modern *Coendou*.

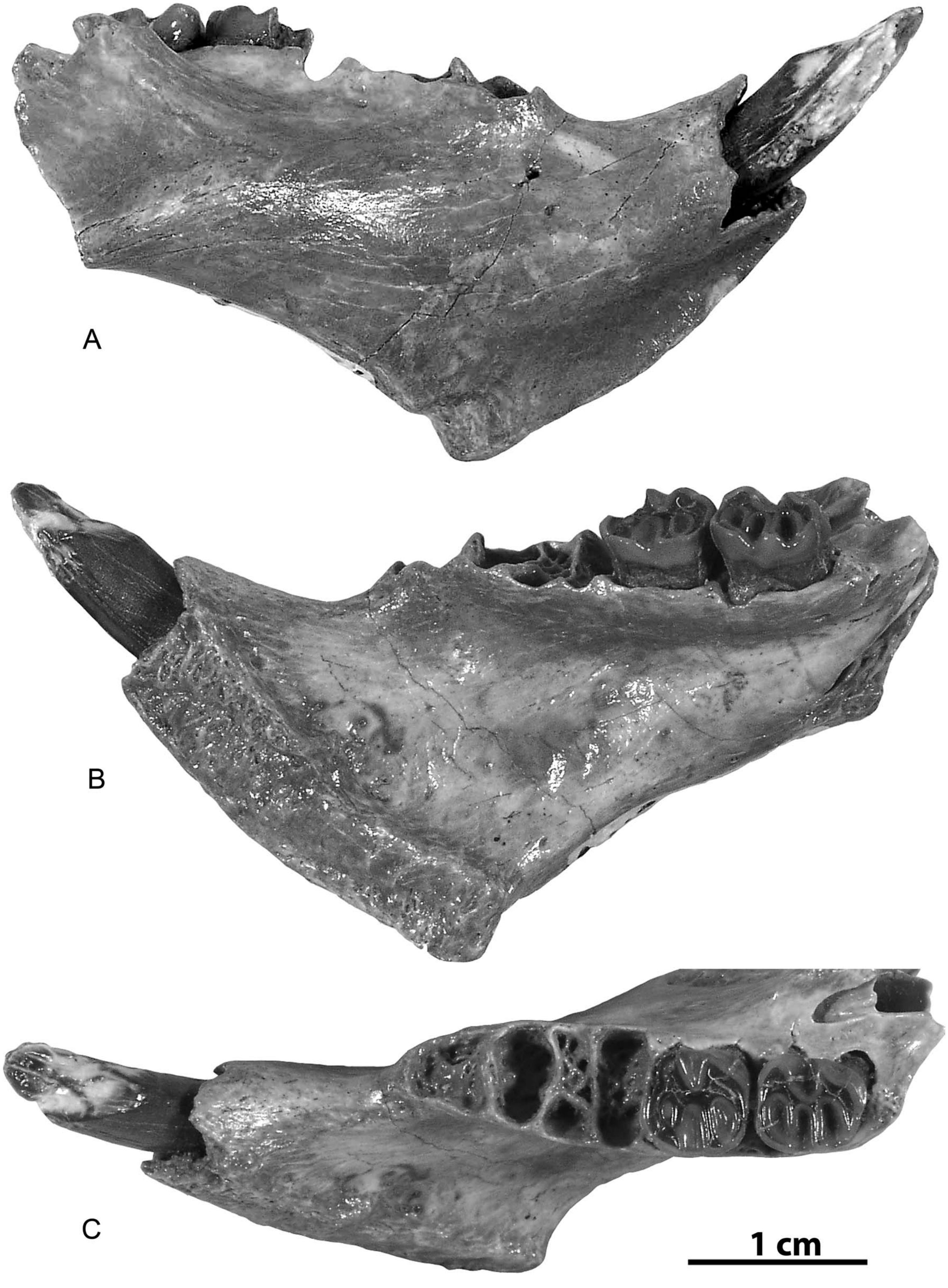

Figure 7 AWC 10858. Fossil right dentary from El Golfo. **A.** buccal; **B.** lingual; **C.** occlusal views.

Figure 8 AWC 12197. Fossil left dentary from El Golfo. **A.** buccal; **B.** lingual; **C.** occlusal views.

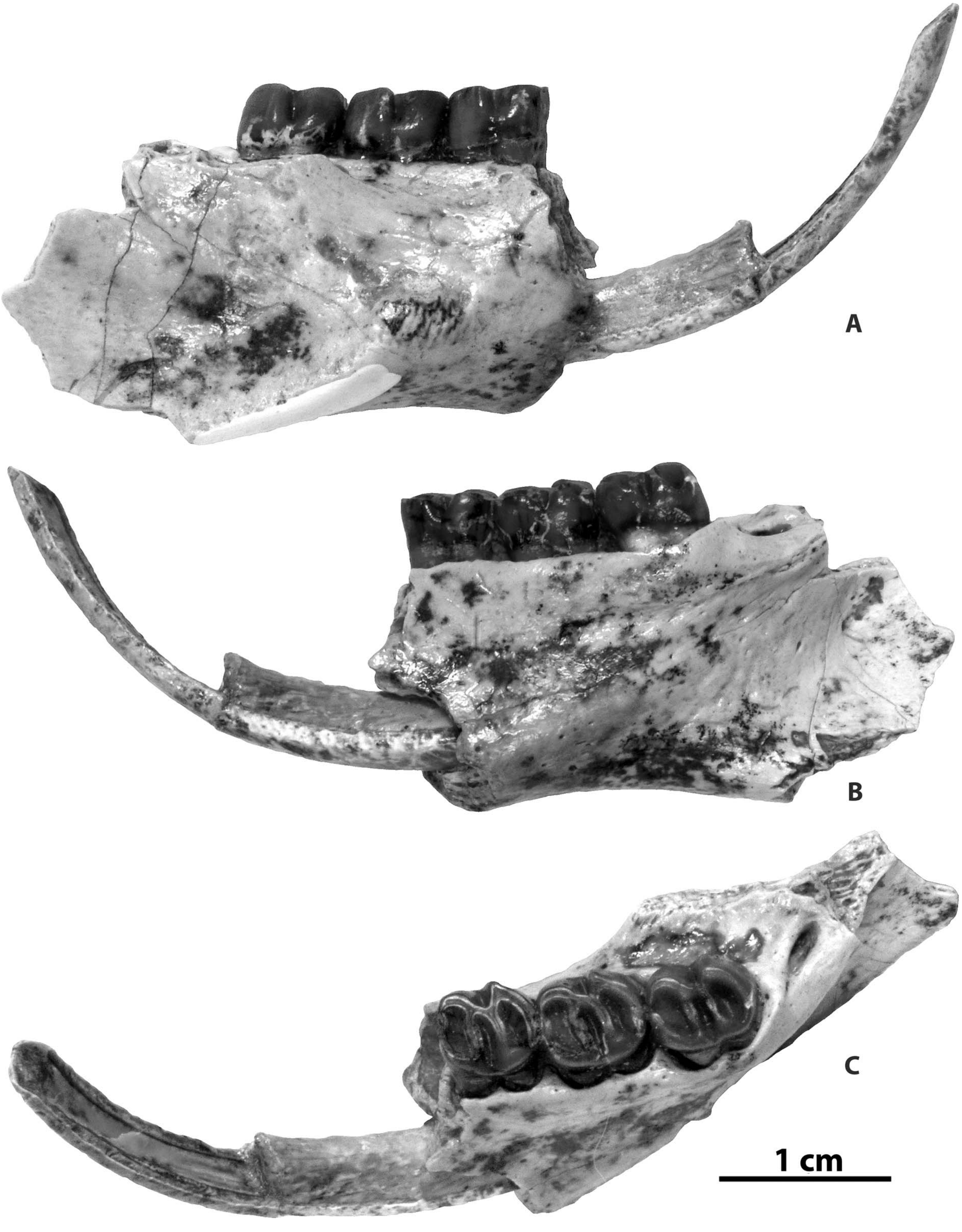

Figure 9 AWC 14810. Fossil partial right dentary from El Golfo. **A.** buccal; **B.** lingual; **C.** occlusal views.

Figure 10 AWC 12540. Fossil partial right humerus from El Golfo. **A.** anterior; **B.** posterior; **C.** medial; **D.** lateral views.

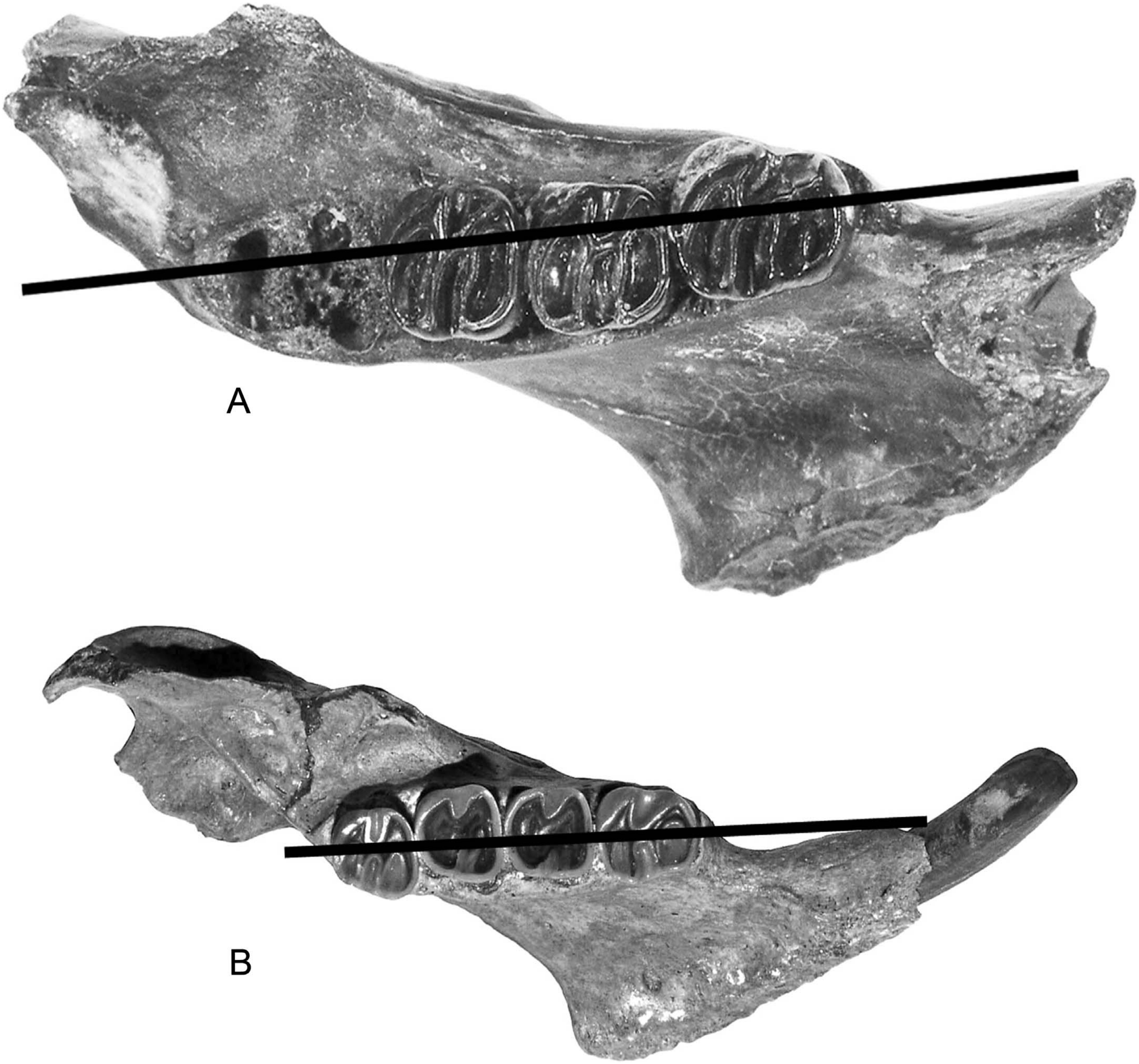

Figure 11 Occlusal view of fossil left dentary from Leisey 3A locality in Florida (UF 124632) **A.** demonstrating cheek-tooth axis extending anteriorly lateral to incisor; and occlusal view of fossil left dentary from Inglis 1A locality in Florida (UF 21473); **B.** also demonstrating cheek tooth axis extending anteriorly lateral to incisor.

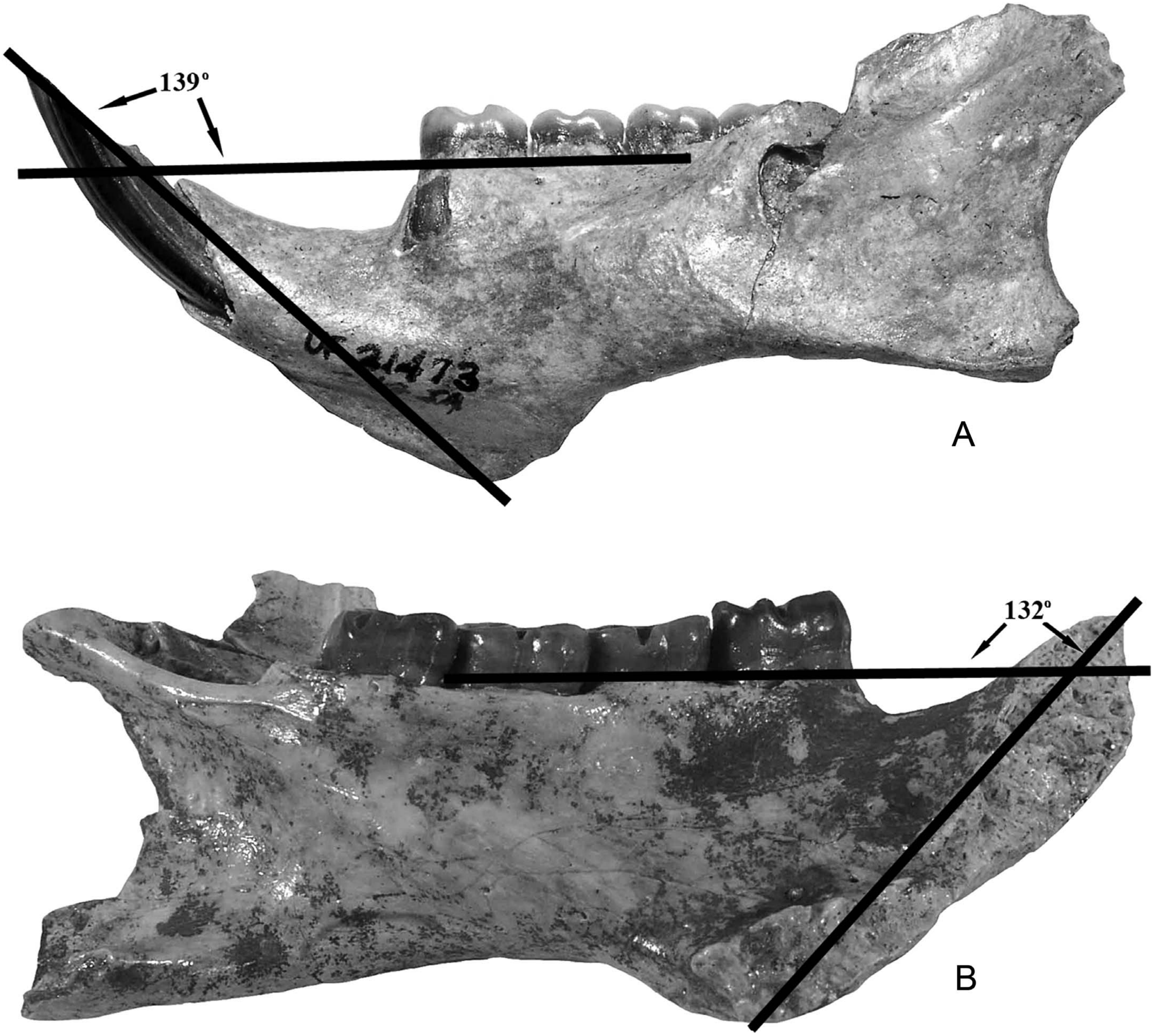

Figure 12 Buccal view of fossil left dentary of *Coendou kleini* (UF 21473) **A.** showing measurement of angle of incisor procumbency: and **B.** lingual view of fossil left dentary of *Erethizon bathygnathum* (UO F-16271) showing measurement of angle of incisor procumbency.

Appendix 1

MUSEUM IDENTIFICATION NUMBERS OF SPECIMENS EXAMINED IN THIS STUDY

Modern Porcupines

Coendou bicolor (n=11): AMNH 15459, 23472, 41204, 214610, 214611, 214612, 214615; FMNH 41204, 65799, 65800; LACM 27376; *C. melanurus* (n=1): AMNH 70120; *C. mexicanus* (n=26): AMNH 29821, 123272, 123273, 123274, 123275, 131727, 135976, 137991, 137992, 139253, 143969, 145983, 186427, 190417, 190418, 190419, 190420, 190421, 190422; FMNH 14897, 15611, 34993, 34994; LACM 24836, 25146, 74306; *C. nycthemera* (n=8): AMNH 96324, 96325, 96326, 96327, 96328, 134075, 134076, 134211; *C. prehensilis* (n=42): AMNH 61785, 70204, 70296, 73680, 134062, 134064, 134066, 134067, 134069, 134070, 134071, 171286, 214613, 214614, 262274; AWC 2; FMNH 20031, 43294, 61862, 61863, 86915, 86916, 86917, 87897, 95783, 122987; PSM 14196, 14197, 14198, 14199, 14200, 14201, 14202, 14203, 14204, 14205, 14206, 14207; MNHN A2859; ZMUC 521, L43, L44; *C. pruinous* (n=2): FMNH 140260, 140261; *C. rothschildi* (n=5): FMNH 14181, 14182, 30742, 30743; LACM 74489; *C. rufescens* (n=13): AMNH 73678, 150028, 181483, 181484; FMNH 47054, 88525, 88526, 88527, 89261, 89262, 89263, 89264, 89266.

Erethizon dorsatum (n=73): AMNH 6740, 9890, 18066, 20773, 20774, 21849, 21891, 22705, 64358, 64359, 64360, 67215, 67890, 120470, 120573, 120574, 120575, 121895, 121896, 122663, 122664; AWC 1; DMNS 247, 931, 1154, 1156, 5037, 6635, 10372; FMNH 18390, 20342, 20344, 30377, 38029, 52898, 58811, 90504, 161432, 167210; LACM 253, 1683, 85250; MNA Z9. 447, Z9.505, Z9.506, Z9.509, Z9.690, Z9.759, Z9.3677, Z9.4168; PSM 2382, 2779, 3077, 5357, 8566, 9513, 9514, 10101, 10102, 16206, 20638, 20927, 24265, 24839, 24842, 24843, 24844, 24845, 26338, 26339, 26341, 26342, 26343.

Fossil Porcupines (Genus as in "Systematics" in This Paper)

Erethizon bathygnathum: USNM 13684; UO F-16271, F-16272; IVCM 309, 460; ABDSP(LACM) 1563/V6136; LACM 61420, 6210; *E. cascoensis*: F:AM 17883-1, 17883-2, 17883-4, 17883-5, 17883-6; *E. dorsatum*: USNM V 7668, V 7669, V 7670, V 7671, V 7672, V 7673, V 8128, V 8130, V 8134, V 25689, V 25690, V 25691; LACM(CIT) 192/2968, 293/2149; LACM 1748, 15091, 150692, 150693, 150694, 150695, 150696, 150697, LACM uncatalogued; UF 21493.

Coendou poyeri: UF 121740, 121747 (from Hulbert 1997); *C. kleini*: UF 21473, 21474, 21475; *Coendou* cf. *C. kleini*: AWC 10858, 12197, 12540, 13592, 14810; IGM 10199; *Coendou* species: MNHM TAR 695, 696; UF 11776, 124632, 135669, 21490, 21492; UMMP V-47106; *C. magnus*: ZMUC Lund 9424, 9429, 9430, 9431, 9433, 9434, 9435, 9436, 9438, 9440, 9441, 9442, 9443; ZMUC E Museo Lundil p. 61 Nr. 31; ZMUC E Museo Lundii p. 63 Nr. 18, Nr. 19, Nr. 20, Nr. 21, Nr. 22, Nr. 23; ZMUC E Museo Lundii plate v Nr. 5 and 6 (images of two caudal vertebrae from an assemblage of 31).

Appendix 2

MEASUREMENT METHODS

All measurements are in millimeters or degrees.

Alveolar length of cheek-tooth row—the straight-line distance from the most anterior portion of the (d)p4 alveolus to the most posterior portion of the m3 alveolus. Measurements were not done if m2 and/or m3 were unerupted.

Premolars and molars—in the A-P direction from the most anterior margin of enamel on the occlusal surface to the most posterior margin of enamel; the lingual-buccal width of the body of the tooth (not the occlusal surface) was measured from the lingual groove to the buccal groove. While this latter measurement does not measure the widest portion of the tooth, it provides fixed landmarks and precludes a potential source of error—the need to estimate the widest portion.

Incisors—measured in relationship to the enameled anterior surface of the tooth, at 90 degrees for the anterior–posterior diameter and parallel for the transverse diameter.

Diastema—from the most anterior margin of the (d)p4 alveolus to the center of the posterior margin of the incisor alveolus. If either of the alveoli appeared broken, the measurement was not done.

Symphysis—a straight line from the most dorsal to the most ventral margins of complete symphyses.

Longitudinal axis of the cheek-tooth row in relation to the incisor—This trait was crucial to White's (1968) argument that the fossils are *Coendou*. He found that the axis was lateral to the incisor in *Coendou* and medial to the incisor in *Erethizon*. However, we had difficulty following his description of the measuring technique (White, 1968). Because the cheek-tooth row and the incisor in a porcupine dentary do not share the same horizontal or vertical plane, the slightest rotation of the jaw will change the orientation of the cheek-tooth axis with respect to the incisor. We measured the axis by photographing the row of cheek teeth with the horizontal plane of its occlusal surface directly under and at right angles to the camera; we then used Adobe Photoshop to draw the axis line from the most distal portion of m3 through the most anterior portion of p4, with the diagnostic end of the line continuing on anteriorly and ending where the incisor emerges from its alveolus. Depending on where in relation to the incisor or its intact alveolus the anterior end of the line terminated, we described the axis as being lateral to the incisor, touching the middle of the incisor, or being medial to the incisor. Because the cheek-tooth row has a slight arc in its shape, this measurement does not bisect the individual teeth (Figs. 3, 11).

Depth of dentary below p4 and m2—for p4, from the anteriormost alveolar rim to the deepest portion of the dentary (at the ventral margin of the symphysis); for m2, from the alveolar rim at the buccal groove to the ventral margin of the dentary at its narrowest portion. We were unable to consistently reproduce these measurements in the same specimens and so will not use the results in this paper.

Extent of anterior projection (procumbency) of lower incisor—We made two measurements of this character, utilizing the line-drawing capabilities of Adobe Photoshop. On the buccal side of the dentary, we measured the angle created by a line drawn anteriorly across the top of the bony alveoli at m1–2, intersecting with a line drawn from the most inferior part of the horizontal ramus (at the ventral end of the symphysis) to the tip of the incisor. If the incisor was absent or broken, we did not do the measurement. On the lingual side, the same horizontal line along the alveoli at m1–2 was used; the intersecting line was drawn from the most ventral portion of the (fully intact) symphysis through the most dorsal portion; the incisor was not included in the measurement, but the incisor alveolus is coincident with the symphysis. These two measurements gave us the ability to measure several fossil dentaries (see Sussman, 2011) (Figs. 2B, 2D, 2F, 2G, 4, 12).

Dental enamel masticatory scratches—examined with a binocular dissecting microscope at 10×, with lighting of the specimen at an angle to accentuate shadows.

Caudal vertebrae—evaluated for total numbers in individual specimens and for the presence or absence of foramina in transverse processes and for bifurcated transverse processes (Figs. 5, 6).